GROWTH AND TROPIC MOVEMENTS OF PLANTS

BY

SIR JAGADIS CHUNDER BOSE

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PREFACE

Plant-physiology has been enriched by contributions to knowledge made by a succession of eminent and devoted workers. In regard to my own investigations on the subject, it may not be out of place to state that, being originally intended for the profession of medicine, I had the great advantage of pursuing at the University of Cambridge the study of the life-reactions of both plants and animals. Since then two subjects have claimed my closest attention—the physics of inorganic and the physiology of living matter.

Being at one time called upon to teach physiology of plants to a student preparing for a University degree in Science, the various questions raised by the unsophisticated mind of my pupil led me to realise that some of the theories which I had passively imbibed in my student days were by no means infallible. I also came to recognise that the main difficulty which stood in the way of deeper knowledge was the absence of sufficiently sensitive means for detecting the internal activities of plant-life. I therefore devoted many years to the invention and construction of various Automatic Recorders of extreme delicacy and precision, which enable the plant itself to write down the inner workings of its life.

Unfounded speculation has often obstructed the advance of knowledge; facts must supersede speculation, for it is not the preconceived bias of the observer, but unimpeachable facts that alone can lead to the establishment of sound theory. This accounts for the attitude of detachment that I maintained for many years. In the preface to my

'Plant Response' (1906) I stated that the aim of my work was the demonstration of the unity of physiological mechanism of the plant with that of the animal, as evidenced by the script of the plant, and not the treatment

of known aspects of plant movements which is to be found detailed, together with the history of the subject, in standard books of reference on plant-physiology, such as those of Sachs, Pfeffer, Strasburger, Darwin, Francis Darwin, Vines and Detmer.

My investigations were commenced with the study of the mechanical response given by plants to stimulation ('Plant Response,' 1906). Since then they have been greatly extended by instrumental appliances of extraordinarily high magnification, the employment of which at one time created some misgiving that the records obtained might be due to physical disturbance and not to physiological reaction. It would be an unpardonable omission of any investigator to fail to take complete precautions against all possible purely physical effects. The obvious method is to perform parallel experiments with two plants, one of which is alive and the other dead. The vigorous response of the living plant, contrasted with complete absence of all response in the dead, gives conclusive evidence in regard to the physiological character of the reaction. This test has been carried out by competent authorities, who reported (*Nature*, May 6, 1920) that my Magnetic Crescograph, with its magnification of one to ten million times, gives correct record of what is undoubtedly the physiological response of the plant.

The results obtained by the method of mechanical response were confirmed in every detail by the method of electric response, the essential feature of which is the negative electromotive variation which is caused by stimulation. In my 'Comparative Electro-Physiology' (1907) special precautions were enjoined for avoiding the errors into which investigators are likely to fall in the employment of these powerful aids to investigation.

I have in this, and in my previous works, employed several independent methods of experimentation, whose

concordant testimony could leave no doubt as to the authenticity of the newly discovered facts. Advanced investigation necessarily depends on the use of specially devised instrumental appliances and on the proper understanding of the technique of new methods, which can only be acquired after sufficient training. The perfect reliability of my highly sensitive instruments has been repeatedly verified at various scientific centres both in the West and in the East. The technical knowledge of the new methods can be gained after a certain amount of practice. Professor Hans Molisch, lately Director of the Plant-Physiological Institute, Vienna University, during his recent visit to my Institute, was able to repeat, with invariable success, many of the experiments described in this volume. His account of some of these will be found in *Nature* of August 4, 1928, and of April 13, 1929.

It must be confessed that I was completely baffled, at the beginning of my researches, by many results which were as astonishing as they were unexpected. It was long persistence and careful comparison of numerous records that ultimately led to the elucidation of all anomalies. Attention had hitherto been centred on the end-effects, which, taken alone, are misleading. Examination of continuous records under prolonged stimulation showed clearly the gradual transformation of what may be regarded as the normal reaction to its very opposite. With such basic facts to work upon, it was afterwards possible to discover the causes of transformation.

I may here briefly refer to a few of the more important results. For instance, the excitation of plants by radiation had come to be regarded as more or less confined within the narrow range of the visible spectrum. Experiments on the effects of wireless waves and of a high-frequency alternating field of electric force prove, on the contrary, that the sensitivity of plants to the ethereal spectrum extends far beyond the intra-red region.

An unexpected factor in the modification of normal

tropic curvature has been discovered in the transverse conduction of excitation across the organ, by which the response becomes gradually transformed from the positive to the negative. The irritability of the root has been found to be in no way different from that of the shoot. A new method for the physiological discrimination of gradation of excitability in different layers of a tissue has led to the discovery that there are certain cells in the lower half of the pulvinus of *Mimosa pudica* which are far more sensitive and active than the rest.

In the investigation of geotropism, the exact direction of the incident stimulus has been determined, as also the fundamental reaction under this mode of stimulation. The device of the Photo-Geotropic Balance has made possible the comparison of the effects of two modes of stimulation on an identical organ. Investigation of the various characteristics of the geotropic reaction has been greatly facilitated by the discovery of geo-electric response, first described in my 'Comparative Electro-Physiology' (1907). The geo-perceptive layer has been localised by the Electric Probe, and a probable explanation had been suggested of the opposite geotropic curvature of the root and the shoot in the experimentally established fact that the stimulation of the responding region of the root is indirect, whereas it is direct in the shoot.

Another important result is the demonstration of the torsional response of dorsiventral organs under different modes of lateral stimulation, and the establishment of the Law of Torsional Response. The extension of this particular method of inquiry has led to the solution of various problems connected with the torsion of twining stems.

Finally, from the fully demonstrated facts that direct stimulation induces contraction while indirect stimulation causes expansion, a wide generalisation has been established, which includes within its scope the diverse tropic movements of plant-organs.

I have endeavoured to link all the observed facts together

by a consistent and logical interpretation. This interpretation may possibly be subject to modification, but it will serve until something better has been suggested. The facts on which the theoretical interpretation is based are, however, irrefutable.

I conclude with an extract from the preface of my 'Comparative Electro-Physiology' (1907) that by the new methods employed not only

> a deeper perception of unity (of physiological mechanism of plant and animal) has been made available, but also many regions of inquiry have been opened out which had at one time been regarded as beyond the scope of experimental exploration.

I take this opportunity to express once more to my assistants and scholars my thanks for the most efficient help rendered in these difficult and prolonged investigations.

J. C. BOSE.

BOSE RESEARCH INSTITUTE, CALCUTTA,
May 1929.

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GROWTH AND TROPIC MOVEMENTS OF PLANTS

CHAPTER I

INTRODUCTORY

Growth and Tropic Movements of Plants

In my 'Motor Mechanism of Plants,' published a year ago, detailed accounts were given of investigations on the motor mechanism of adult members such as the leaves of sensitive and other plants. A very large and extensive class of phenomena still remained to be dealt with, namely, the movements of growing organs induced under external stimulation. The consideration of these responsive movements of growing organs forms the main subject of the present volume.

The movements induced in a growing organ by external stimulation are extremely diverse. The effective agents are manifold—the stimulus of contact, of electric current, of gravity, of radiation visible and invisible, and the rise and fall of temperature. They may act on organs which exhibit all degrees of physiological differentiation, from the radial to the dorsiventral. An identical stimulus sometimes induces one effect, and at other times precisely the opposite. Thus under unilateral stimulation by light of increasing intensity, a radial organ exhibits first a positive, then a dia-phototropic, and finally a negative movement.

the positive movement is towards, and the negative away from the stimulus. Strong sunlight brings about a paraheliotropic movement, often described as the 'Midday sleep,' in which the apices of leaves or leaflets turn either towards or away from the source of illumination. In the leaflet of *Averrhoa Carambola* the movement is downward, whichever side is illuminated with strong light; in the leaflet of Mimosa the movement under similar circumstances is in the opposite direction. Such photonastic movements, apparently independent of the directive action of light, have been regarded as phenomena unrelated to phototropic reaction, due to a different kind of irritability with a different mode of response. Pfeffer,[1] after enumerating the apparently anomalous effects induced by light, which is only one out of numerous factors in operation, dwells on the inadequacy of the various explanations that have been advanced, and concludes by saying that 'the precise character of the stimulatory action of light has yet to be determined. When we say that an organ curves towards a source of illumination because of its heliotropic irritability, we are simply expressing an ascertained fact in a conveniently abbreviated form, without explaining why such curvature is possible or how it is produced.'

Greater difficulties are encountered in explaining the effects of other modes of stimulation. An attempt is made in this volume to discover and explain the common and fundamental reaction which underlies the various responses given by growing organs under all modes of unilateral stimulation which induce tropic curvature. The tropic movements are essentially due to unequal growth induced in the two opposed sides of the organ. What now are the characteristic modifications of growth at the proximal and distal sides of the organ under various modes of stimulation? Do they induce reactions essentially similar or specifically different?

[1] Pfeffer, *Physiology of Plants*, trans. by A. J. Ewart, vol. ii, p. 71 (Clarendon Press).

In spite of much theorising, no clear idea has yet been reached concerning the ultimate mechanism of growth in the individual cell. It is not possible to go beyond the statement that the growth of the cell depends upon its turgidity, the degree of which, and also the rate of growth, are regulated by the cell-protoplasm. Fundamentally, therefore, the mechanism of growth is the same as that of other plant-movements.

For the purpose of observing the rate of growth in length, auxanometers magnifying about 20 times have been in general use. Even with this magnification it takes several hours to measure the rate of growth and the change induced in it by any particular stimulus. The external conditions cannot, however, be maintained constant for such a protracted period, and the observed result is vitiated by the effect of change in these factors.

The possibility of accurate investigation, therefore, lies in reducing the period of the experiment to a few minutes during which the external conditions can be maintained constant, thus making possible the accurate determination of the variation of rate of growth induced by any one mode of stimulation. This necessitates the devising of a method of high magnification for the record of growth.

Among the subjects discussed in the present volume are :

1. Absolute determination of the rate of growth by several sensitive and exact methods.

2. Quantitative determination of changes induced in growth under variation of external conditions.

3. The modifying influence of tonic condition on response to external stimulation.

4. The effect of radiant energy through a wide range of the ethereal spectrum.

5. The effects of direct and indirect stimulation on growth.

6. Tropic curvature under unilateral stimulation.

7. The modification of tropic curvature by transverse conduction of excitation.

8. The relative effect of unilateral stimulation of shoot and root.

9. Thermonastic and thermo-geotropic phenomena.

10. Mechanical and electric response under geotropic stimulation.

11. Torsional response under lateral stimulation.

12. Phenomenon of autonomous torsion.

CHAPTER II

THE HIGH MAGNIFICATION CRESCOGRAPH

The essential difficulty in investigations on growth arises from its extraordinary slowness. The average rate of longitudinal growth in a plant is about $\frac{1}{100000}$ inch per second, a length which is half that of a single wave of sodium light. Even with the magnifying growth-recorders hitherto employed, it takes several hours to detect and measure its rate. For the accurate investigation of the effect of any given agent on growth, it is necessary to keep all other conditions, such as light and heat, strictly constant throughout the experiment: even if this were possible, there would probably be some autonomous variation of the rate of growth during such lengthy periods. Considerable uncertainty is inevitable in results obtained by a method which involves a long time for observation. The element of uncertainty can only be eliminated by reducing the period of the experiment to a few minutes, but that necessitates devising a method of very high magnification and an automatic record of the magnified rate of growth.

The Optical Lever

The problem of high magnification was first solved by the employment of my Optical Lever, where an axis carrying a mirror undergoes rotation proportional to the growth elongation. The reflected spot of light magnified the movement of growth from 1000 to 10,000 times. The vertical movement of the spot of light was converted into

a horizontal movement by means of a mirror suitably inclined. The excursion of the spot of light was followed by means of a pen on a drum revolving at a known rate; or the record was obtained automatically by photography. Hence a curve was obtained whose ordinate gave growth-movement, and the abscissa time.[1]

Records thus obtained opened out a very extensive field of investigation on growth and its variation under the manifold influences of the environment. The photographic method is automatic, but it necessitates the discomfort and inconvenience of a dark room; the results, moreover, cannot be followed visually. The other method of obtaining the curve of growth by following the excursion of the spot of light with a pen is far more convenient, but the results in this case are likely to be affected by personal error. In order to obviate all these difficulties I devised a direct method, in which the plant by its own autograph exhibits the absolute rate of growth and any induced variation in an extremely short period of time.

The Automatic High Magnification Crescograph

I secured high magnification by means of a compound system of two or more levers.[2] The plant is attached to the short arm of a lever, the long arm of which is attached to the short arm of the second lever. If the magnification by the first lever be m, and that by the second n, then the total magnification will be mn.

The numerous practical difficulties encountered were principally due (1) to the great tension exerted by the two levers on the plant; (2) to the possible stretching of the connectors by which the plant is attached to the first lever, and the first lever to the second; and (3) to the friction at the fulcrums. I will describe the most recent method employed to overcome these difficulties.

[1] *Plant Response* (1906), p. 112.
[2] *Proc. Roy. Soc.*, B vol. 90 (1919), p. 365.

Weight of the levers.—The tension exerted by the weight of even low magnification auxanometers is found to modify the normal rate of growth. In the compound system of levers employed in my apparatus, the first lever has to be made rigid in order to exert a pull on the second without undergoing any bending. In order to secure the rigidity first lever, it must have a certain minimum cross-n. This entails not only an increase of weight and sion on the plant, but also increased friction at the m. The conditions necessary to overcome these alties are: (1) construction of a very light lever ssing sufficient rigidity, and (2) arranging the two s in such a way that the tension on the plant may be ced to any extent desired, so as practically to eliminate It may be stated here that the second lever serving he writer can be made of fine glass fibre of extreme tness.

For the construction of the first lever I use 'navaldum,' well-known alloy of aluminium which possesses con-erable rigidity. A thin strip of this material about cm. in length is taken, rigidity being imparted to it by ing it a T-shape. A specially prepared thin strip of mboo has been found to be a satisfactory substitute for e metal.

Each of the two levers is nearly balanced by a counter-se W (fig. 1). The horizontal fulcrum-axis of each lever supported in a fork provided with appropriate jewel-arings.

Attacher and Connector.—The first of these terms signates the contrivance for connecting the plant with e first lever, and the second, the flexible connection tween the first and the second lever. For the *Attacher* use a thin glass hook, which does not stretch, nor does undergo any appreciable change of length on variation temperature. The upper end of the hook can be placed notches in various positions on the first lever, greater nification being produced when the hook is brought

nearer the fulcrum. The *Connector*, which joins the first to the second lever, has to be flexible. For this I employed different devices, of which the following is simple and effective. The connection is made by a thin waxed string which has been previously kept stretched for several days by a weight. A moderate tension does not stretch the prepared string any further, nor is the string affe
any hygroscopic change.

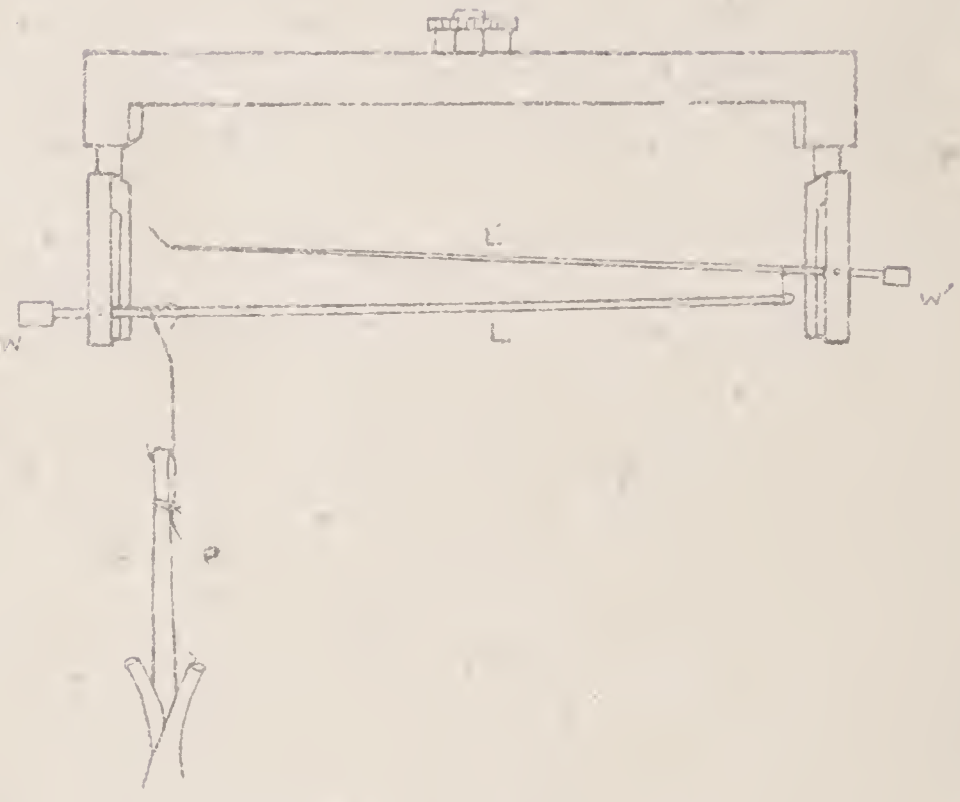


FIG. 1. Compound lever of High Magnification Crescograph

P, plant attached to arm of lever, L; L′, second lever with bent tip for tracing record; W, W′, balancing counterpoise; each lever is carried by a fork; the transverse fulcrum-bar of the lever ends in pin-points which rest in agate cups one on each side of the fork.

The attachment of the plant to the first lever may to the short arm of the lever, in which case the grow elongation is recorded as a down-curve. It is pern more natural to associate upward growth with an up-cu this may be secured by attaching the plant to the arm of the lever (fig. 1). The curvature in the recor slight, and is practically negligible in the middle por of it.

Automatic Record of the Rate of Growth

Another obstacle to obtaining an accurate record of the curve of growth arises from the friction of contact of the bent tip of the writing lever with the recording smoked surface of glass. This difficulty was removed by an oscillating device (fig. 2); the smoked glass plate G is made to oscillate, to and fro, at right angles to the tip of the writing lever; the oscillations are at regular intervals, say once in a second. The bent tip of the writer thus comes periodically into contact with the recording plate during its extreme forward movement. The record of growth therefore consists of a series of dots, the distance between them representing magnified growth during a second.

The approach of the recording surface to the writing r has to be rendered very gradual, otherwise the sudden oke of the plate causes an after-oscillation of the writing er, resulting in multiple dots which spoil the record. order to obviate this, a special contrivance had to be vised by which the speed of approach of the plate was adually reduced to zero on contact with the writer; te of recession should, on the other hand, continuously ase from zero to maximum. The writer will in this ner be gently pressed against the glass plate, marking dot, and then set free. It is only by strict observance these conditions that the disturbing effect of after-bration of the lever can be obviated.

The oscillating device consists of an eccentric E, a crank K actuated by clockwork, and a slide S, supported on ball-bearings, which carries the smoked glass plate. The eccentric consists of a cylindrical rod of glass mounted centrically. A semi-rotation of the eccentric in one ection pushes the recording plate gradually forwards, ile that in the opposite direction causes it to recede g. 2). The eccentric is actuated by the crank K, which its turn is acted on by clockwork which releases a re-lving wheel at intervals of 1, 2, 10 or 15 seconds, according

to the requirement of the particular experiment. The complete apparatus is seen in fig. 3, in which the revolving wheel for actuating the oscillating mechanism is clearly shown.

I used at first a pair of parallel eccentrics, but in the newest type of apparatus with improved to-and-fro sliding arrangement, one eccentric is found to be quite sufficient. A very important condition for success is the securing of

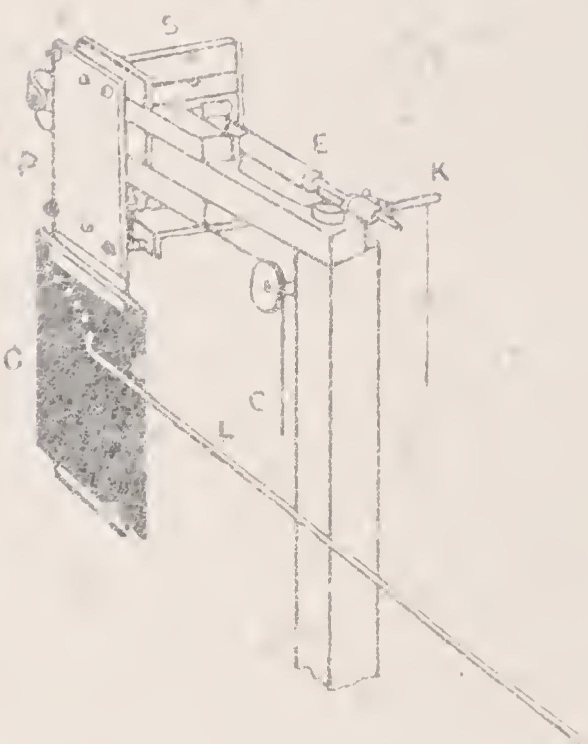


FIG. 2. Mechanism for oscillation of plate.

E, eccentric; K, crank; S, slide; P, holder for glass plate G; L, recording lever. Clock releases string, C, for lateral movement of the plate.

perfect smoothness of movement during the oscillation of the plate. A horizontal slide, moving on ball-bearings, carries the vertical plate-holder. The slide is so perfect in action that a puff of air is by itself sufficient to move the free plate-carrier either backward or forward. The plate may thus be maintained in its to-and-fro oscillation with very little expenditure of force, and the power required from the clockwork is therefore very small. In my later instruments an electric oscillating device has been successfully employed, which simplifies the matter still further. An electric current flows intermittently through a coil

wire which sucks in a rod of soft iron attached to the plate-carrier. The force required for bringing about the oscillatory movement thus acts directly, without any intervention of the eccentric.

The amplitude of oscillation of the plate is about 3 mm. It is important that the vertical recording plate should be

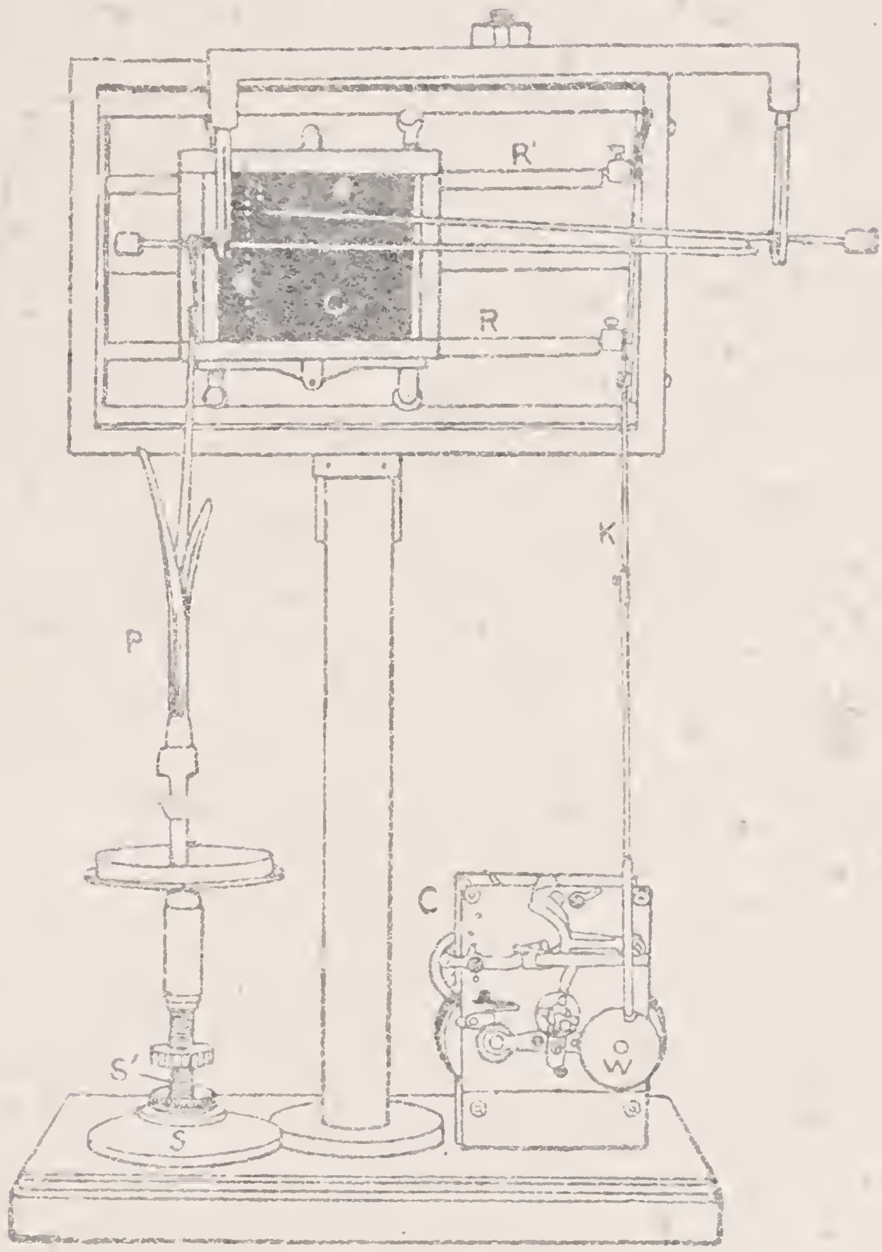


FIG. 3. Complete apparatus.

P, plant; S, S', micrometer screws for raising or lowering the plant; C, clockwork for periodic oscillation of plate; W, rotating wheel.

so adjusted that its distance from the tip of the writer will remain the same during the excursion of the index, as well as during the lateral displacement of the plate moved by the clockwork. Failure to secure this makes the dot-marks unequally distinct; in the worst cases some of the dots

may even be missing. The difficulty is obviated by accurate adjustment of the plate in a vertical plane by means of regulating screws.

Experimental Accessories

The soil in a flower-pot is liable to be disturbed by irrigation and the record be consequently vitiated. This is obviated by wrapping the root, imbedded in a small quantity of soil, in a piece of cloth, the lower end of the plant being held securely by the clamp of the plant-holder. In order to subject the plant to the action of gases and vapours, or to variation of temperature, it is enclosed in a cylindrical chamber constructed of a sheet of mica, with an inlet and an outlet pipe. The chamber is maintained in a humid condition by means of a sponge soaked in water. Vapours and gases can be easily introduced or removed from the plant-chamber; variation of temperature is simply effected by blowing in heated or cooled water-vapour.

Any quickly growing organ of a plant will be found suitable for the following experiments: complications arising from circumnutation may be avoided by employing either radial organs, such as flower peduncles, buds, or the pistils of certain flowers, or the limp leaves of various species of grass. It is advisable to select specimens in which the growth is fairly uniform. I append a representative list of different specimens in which, under favourable conditions of season and temperature, the rate of growth may be as high as those given below:

Table I.—Average Rate of Growth in Different Specimens.

Peduncle of Zephyranthes .	6·7	mm.	per	hour
Leaf of grass . .	1·10	,,	,,	,,
Pistil of Hibiscus flower . .	1·26	,,	,,	,,
Seedling of Wheat . .	1·00	,,	,,	,,
Flower-bud of Crinum .	2·20	,,	,,	,,
Seedling of Scirpus Kysoor .	3·00	,,	,,	,,

The specimen employed for experiment may be an entire plant; it is, however, more convenient to make

a detached organ, the exposed cut end being wrapped in a moist cloth. The shock effect of section disappears in the course of a few hours, after which the isolated organ renews its normal rate of growth. Of the different specimens, the plant *Scirpus Kysoor* offers special advantages; its leaves are much stronger than those of Wheat and other grasses and can bear a certain amount of pull without harm. The rate of growth under favourable seasonal conditions is considerable: some specimens were found to have grown more than 8 cm. in the course of 24 hours, or more than 3 mm. per hour. This was during the rainy season in the month of August; but a month later the rate of growth had fallen to less than 1 mm. per hour.

I will now describe certain typical experiments which will show (1) the extreme sensibility of the Crescograph and (2) its wide applicability in different investigations. The capability of the apparatus in the accurate determination of the time-relations of responsive changes in the rate of growth will be described in a later chapter.

In order to ensure regularity in the rate of growth, the plant should be kept in uniform darkness or in uniformly diffused light. So sensitive is the recorder that it shows a change of growth-rate due to the slight increase of illumination caused by the opening of an additional window. One-sided light should be avoided, as it gives rise to disturbing phototropic curvature. Temperature and hygrometric condition must be kept constant. After observing these precautions, the growth rate of vigorous specimens is found to be very uniform.

The records are taken either on a stationary plate or on a plate which moves past the writer at a uniform rate.

Stationary Plate Method.—A record, which is vertical, is first taken, to ascertain the normal rate of growth. Then, in order to study the effect of some changed condition, the recording plate is moved 1 cm. to the left; the tip of the writer is brought once more to the bottom by means of the fine screw adjustment S (*see* fig. 3) and another record

taken. The increase or diminution of the space between successive dots in the second record, as compared with the first, at once demonstrates the stimulating or depressing nature of the changed condition.

Moving Plate Method.—The smoked glass plate in this case, as already stated, is carried laterally past the writer. The record is now a curve, the ordinate representing growth-elongation and the abscissa the time. The increment of length divided by the increment of time gives the absolute rate of growth at any part of the curve. As long as the growth is uniform, so long the slope of the curve remains constant. When an agent enhances the rate of growth, there is an upward flexure in the curve; a depressing agent, on the other hand, lessens its slope.

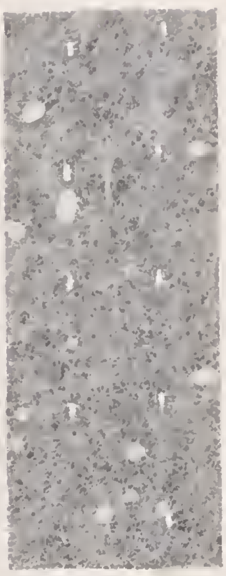


FIG. 4. Crescographic records, with a stationary plate of the absolute rate of growth. Second record taken after 15 minutes. Magnification 10,000 times. (Kysoor.)

DETERMINATION OF ABSOLUTE RATE OF GROWTH

Experiment 1.—The record of growth obtained with a vigorous specimen of *S. Kysoor* on a stationary plate is given in fig. 4. The oscillation frequency of the plate was once in a second, the magnification employed being 10,000 times. The magnified growth-movement was so rapid, that the record consists of a series of short dashes instead of dots.

After the completion of the first vertical record, a second record was taken after an interval of 15 minutes. The magnified record for 4 seconds is 38 mm. in the first record: it is precisely the same in the record taken 15 minutes after. The growth-elongation during successive intervals of 1 second is practically the same throughout, being 9·5 mm. This uniformity in the spacings demonstrates not only the regularity of growth under constant conditions, but also

the reliability and perfection of the apparatus. It also shows that by keeping the external conditions constant, the normal growth-rate can be maintained uniform for at least 15 minutes. As the growth when magnified 10,000 times is nearly 1 cm. per second, and as it is quite easy to measure 0·5 mm., the Crescograph permits the record of a growth-elongation of 0·00005 mm., that is to say, the sixteenth part of a wave of red light. The absolute rate of growth, moreover, can be determined for a period as short as 0·05 second.

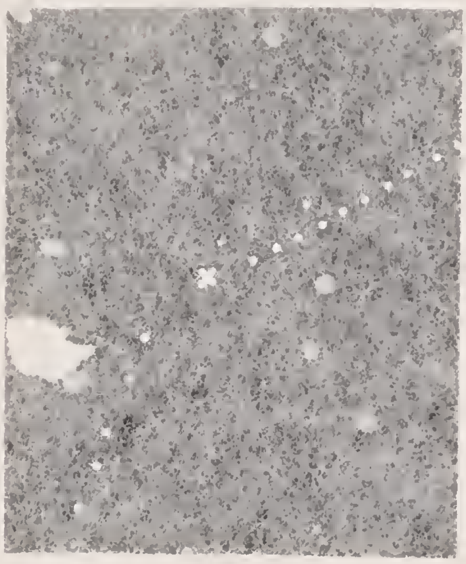


FIG. 5. Effect of temperature.

Record on moving plate, where diminished slope of curve in the second part denotes retarded rate under cold (Kysoor).

These facts will give some idea of the great possibilities of the Crescograph for investigations on growth.

As the period of the experiment is very greatly shortened by the method of high magnification, I have, in the determination of the absolute rate of growth, adopted a second as the unit of time and μ or micron as the unit of length—the micron being 0·000001 metre, or 0·001 mm.

If m be the magnifying power of the compound lever and l the average distance between successive dots in millimetres at intervals of t seconds, then:

$$\text{Rate of growth} = \frac{l}{mt} \times 10^3\ \mu \text{ per sec.}$$

In the record given $l = 9.5$ mm., $m = 10,000$, $t = 1$ secon
Hence rate of growth

$$= \frac{9.5}{10,000} \times 10^3 \mu \text{ per second} = 0.95 \mu \text{ per sec.}$$

I will now give a few typical examples of the emplo
ment of the Crescograph for the investigation of growt
the first example demonstrates the influence of temperatu

Experiment 2. *Effect of lowering the temperature.*—T
specimen employed was Kysoor, and the record was tak
on a moving plate. The first part of the curve represe
the normal rate of growth; moderate cooling produce
diminished slope of the curve (fig. 5), demonstrating t
retardation of growth induced by cold.

Precaution against Physical Disturbance

Experiment 3.—There may be some misgiving abo
the employment of such high magnification; it may b
thought that the accuracy of the record might be vitiat
by physical disturbance, such as vibration. In physic
experimentation far greater difficulties have been ove
come, and the problem of securing freedom from vibrati
is not at all formidable. The whole apparatus needs only t
be placed on a heavy wooden bracket screwed on to the wa
to ensure against mechanical disturbance. As an addition
precaution, a thick sheet of felt is interposed between th
base of the Crescograph and the surface of the bracket t
function as a shock-absorber. To what extent this freedo
from mechanical disturbance has been realised will be foun
from the inspection of the first part of the record in fig. 6
taken on a moving plate. A thin dead twig was substitut
for the growing plant, and a perfectly horizontal record n
only demonstrated the absence of growth-movement b
also of all disturbance. There is also another element o
physical change, against which precaution has to be tak
in experiments on variation of the rate of growth wi

rising temperature. In order to determine its character and extent, a record was taken, with a dead twig, of the effect of raising the temperature of the plant-chamber through 10°. The record, with a magnification of 2000, shows that there was an expansion during the rise of the temperature, after which there was a cessation of physical movement, the record becoming once more horizontal. The obvious precaution to be taken in such a case is to wait for several minutes for the attainment of steady temperature. The movement caused

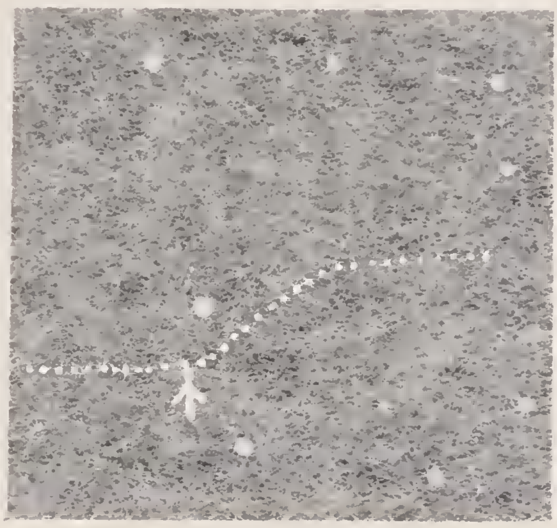


Fig. 6. Effect of variation of temperature on a dead branch, taken on moving plate.

Horizontal record shows absence of growth and freedom from physical disturbance. Physical expansion on application of heat at arrow is followed by horizontal record on attainment of a steady temperature. (Magnification 2000 times.)

by physical change abates in a short time, whereas the change in the rate of growth brought about by physiological reaction is persistent.

Having demonstrated the extreme sensitiveness and reliability of the apparatus for quantitative determination, I now demonstrate its wide applicability for various researches relating to the influence of external agencies in modification of growth.

Experiment 4. *Effect of variation of temperature on growth.*—The record was taken on a stationary plate with a different specimen of Kysoor. The magnification was reduced to 2000; but the interval between successive dots

was increased to 5 seconds. The middle record N (fig. 7) was taken at the temperature of the room. The temperature was next lowered by a few degrees and the record C shows the result. Finally, the record H was obtained when the temperature was raised a few degrees above that of the room. It will be seen that under the action of cold the space between successive dots became shortened, exhibiting a diminution in the rate of growth. Heat, on the

FIG. 7.

FIG. 8.

FIG. 7. Effect of temperature recorded with stationary plate. N, normal rate; C, retarded rate under cold; H, enhanced rate under heat. (Kysoor.)

FIG. 8. Record of a single growth-pulse of Zephyranthes. (Magnification 10,000 times.)

other hand, caused a widening of the interval between successive dots, thus demonstrating enhancement of the rate.

Calculating from the data supplied by the record:

The absolute value of normal rate is	0·457 μ per sec.
Diminished rate under cold . .	0·101 μ ,, ,,
Enhanced rate under heat . .	0·737 μ ,, ,,

Experiment 5. *Pulsation in growth.*—As a further example of the capability of the Crescograph, I give the

record of a single pulse of growth obtained with the peduncle of *Zephyranthes sulphurea* (fig. 8). The magnification employed was 10,000 times, the successive dots being at intervals of 1 second. It will be seen that the growth-pulse commenced with a sudden elongation, the maximum rate being 0·4 μ per second. The pulse of elongation exhausted itself in the course of 15 seconds, after which there was a partial recovery lasting for 13 seconds, the period of the complete pulsation being 28 seconds. The resultant growth is therefore the difference between the elongation and the recovery. Had not a very highly magnifying arrangement been used, the growth would have appeared to be continuous; this is especially the case when the rate is very high. Less favourable conditions appear to promote exhibition of the pulsation, instances of which will be described later.

The Magnetic Crescograph

The highest magnification obtained with two levers is, as already stated, 10,000 times. It might be thought that further magnification would be possible by a compound system of three levers. There is, however, a practical limit to the number of levers that can be employed. The slight overweight of the last lever becomes greatly multiplied, exerting considerable tension on the plant and thus interfering with the normal rate of growth. The friction at the bearings also becomes increased, obstructing the free movement of the writing lever. For securing further magnification, the idea of more material contacts had to be abandoned. A method of magnification without additional contact had therefore to be devised. A magnetised rod of steel was made to function as the first lever, the magnified movement of which causes a very large deflection of a delicately suspended astatic system of magnets. The indicator is a spot of light reflected from a mirror carried by the deflected astatic system. The magnetic lever itself gives a magnification of 50 times, and

the deflected system a further magnification of 20,000 times, the total magnification being thus a millionfold. This was verified by moving the short arm of the lever through 0·005 mm., by means of a micrometer screw. The resulting deflection of the spot of light at a distance of 4 metres was then found to be 5000 mm. or a total magnification of a million times. With a more sensitive apparatus the magnification was increased even to 50 million times.[1]

A concrete idea of this order of magnification is formed when it is realised that this is 30,000 times greater than that produced by the highest powers of the microscope. With such a magnification a single wave of sodium light would appear lengthened to about 3000 cm.

Demonstration by Magnetic Crescograph

With this apparatus I have been able to give striking demonstrations of various phenomena of growth before large audiences at different scientific centres. Employing even the slowly growing flower-bud of the Crinum Lily (the average rate of growth of which is only 0·0006 mm. per sec.), a magnification of a million times was found to be more than ample. The excursion of the indicating spot of light exhibiting the movement of growth was found to be 300 cm. in 5 seconds, the scale being placed at a distance of 4 metres. The temperature of the room was 30° C.

Experiment 6.—The plant-chamber was then cooled to 26° C. by the blowing in of cool water-vapour. The time taken by the spot of light to traverse the 300 cm. length of the scale was now 20 seconds, the growth-rate being thus depressed to one-fourth. Under continuous lowering of temperature the rate was slowed down till there was arrest at 21° C. Warm vapour was next introduced which gradually raised the temperature of the chamber to 35° C. The spot of light now rushed across the scale in a second and a half, that is to say, growth was enhanced to more

[1] *Plant Autographs* (1927), p. 95.

about three times the normal rate. The entire series of the above experiments on the effect of temperature on growth was thus completed in less than 15 minutes.

SUMMARY

The High Magnification Crescograph gives automatic record of growth at a magnification of 10,000 times. Growth movement as minute as the sixteenth part of a wave-length of red light can thus be detected.

Growth appears to be a pulsatory phenomenon. The resultant growth in each pulsation is the difference between elongation and recovery.

The influence of external conditions on variation of rate of growth is recorded by two methods.

In the STATIONARY METHOD the increase or diminution of the distance between successive dots of the vertical record demonstrates the stimulating or depressing nature of the changed condition.

In the MOVING PLATE METHOD the record is a curve, the ordinate representing growth-elongation, and the abscissa, time. A stimulating agent causes an upward flexure of the normal curve; a depressing agent, on the other hand, lessens the slope of the curve.

The Magnetic Crescograph makes possible the demonstration of the principal phenomena of growth and its variations before a large audience, the magnification produced being from one to fifty million times.

CHAPTER III

THE BALANCED CRESCOGRAPH

The Crescograph described in the previous chapter gives records of the enhancement or depression of the rate of growth induced by external change. The enhancement of growth is shown by the increase of spacing between the successive dots of the vertical record taken on a stationary plate, or by the upward flexure of the curve inscribed on a moving plate. Depression of the rate is, on the other hand, indicated by the shortening of the distance between the successive dots or by the downward flexure of the curve.

Though these methods are highly sensitive, yet it requires very careful inspection of the records to detect a change induced in the rate of growth, when such a variation is very slight. It was therefore necessary to devise a new method which would instantly show, by the up or down movement of an indicator, the accelerating or retarding effect of an external agent. For this purpose I first employed the Optical Method of Balance,[1] which was considered at that time to be very sensitive. The spot of light reflected from the Optical Lever (which magnified the rate of growth) was made to fall upon a second mirror to which a compensating movement was imparted, so that the light-spot, after double reflection, remained stationary. Any change in the rate of growth—an acceleration or a retardation—was detected by the movement of the hitherto stationary spot of light, in one direction or the other.

A still more perfect apparatus was next devised which possesses several important advantages; the ex

[1] *Plant Response* (1906), p. 413.

is here secured with ease and certainty; the apparatus has an attached scale which indicates the actual rate of growth, and the upsetting of the balance by a stimulant or a depressor is automatically recorded.

Principle of the Method of Balance

The plant is made to descend at the exact rate at which its growing tip is rising: the latter is attached in the usual manner to the High Magnification Crescograph. When growth is exactly balanced, the record is a horizontal line instead of an ascending curve as in the ordinary method. The apparatus so adjusted is found to be extremely sensitive. The minutest change induced in the rate of growth by the environment is at once indicated by the upset of the balance and recorded as an up- or a down-curve.

The compensating movement of descent.—A regulating contrivance had to be devised for the subsidence of the plant at the same rate as its growth-elongation. The required method is somewhat analogous to the compensating device for an astronomical telescope, which neutralises the effect of the earth's movement round her axis once in 24 hours. The problem is, however, far more difficult; for instead of compensating for a definite rate, adjustments had to be made for balancing widely varying rates of growth of different plants, and even of the same plant under different conditions. The problem was solved by the employment of two different methods of compensation: A, the Method of Falling Weight, and B, the Method of Inclined Plane.

A. Method of Compensation by Falling Weight

By means of a train of revolving clock-wheels actuated by the fall of a weight, the plant is made to subside at the same rate as that at which it is growing.[1] It will be presently explained how the gradual turning of the adjusting screw S in a right-handed or a left-handed direction causes a continuous

[1] *Life Movements in Plants* (1918), p. 257.

decrease or increase in the rate of the compensating fall (fig. 9). Growth thus becomes accurately balanced, so that the tip of the plant remains exactly at the same level.

I take a concrete example in explanation of the adjustment for compensation. Different plants exhibit considerable difference in the rate of their growth ; in a large number

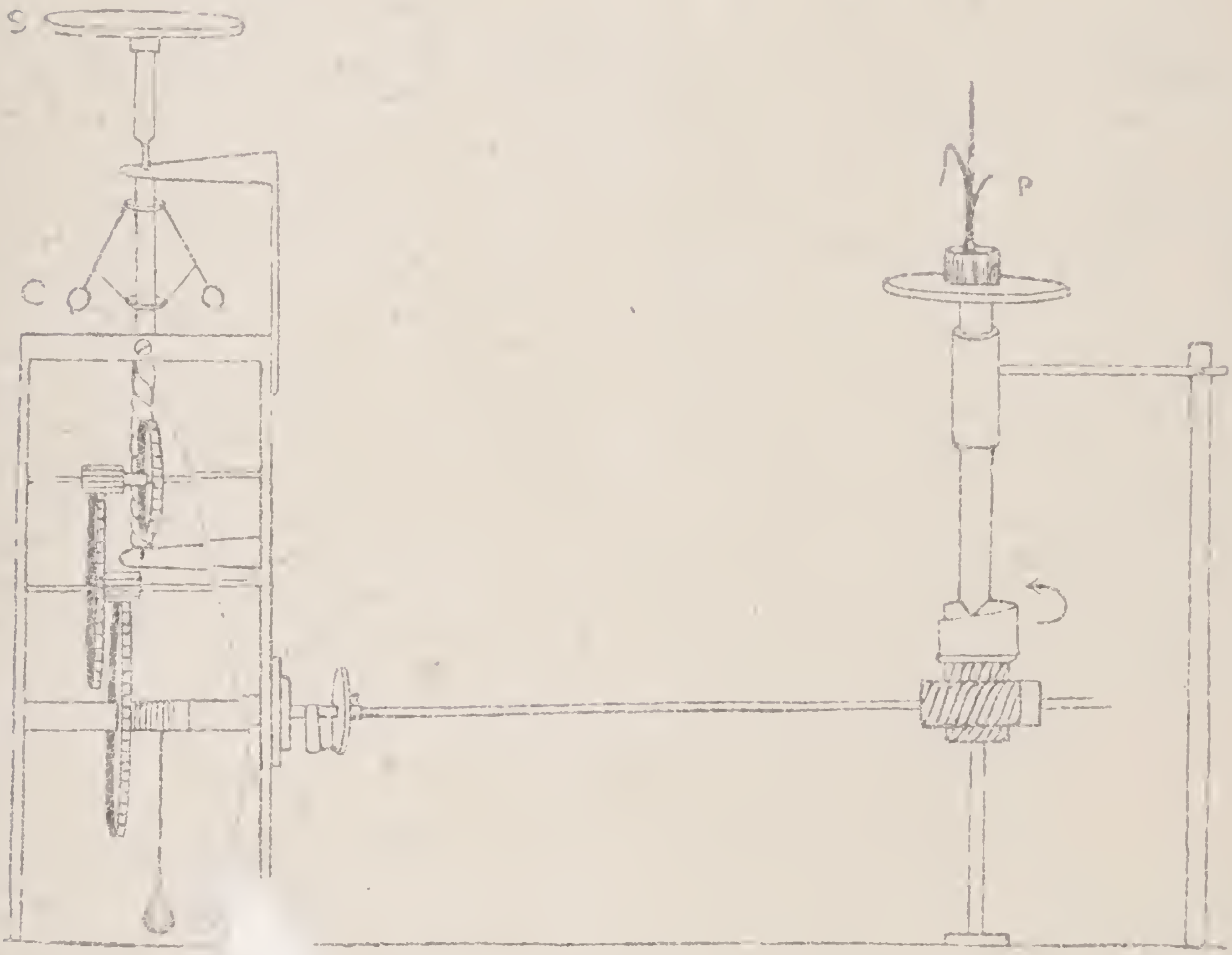


Diagram of Method of Falling Weight.

Compe[illegible] growth movement effected by equal subside[illegible] holder supporting the plant (P). Adjusting screw [illegible] the speed of the governor (G), and the rate of su[illegible] of the plant. W, heavy weight actuating clockwork.

of cases the rate varies from $0 \cdot 17\,\mu$ to $1 \cdot 0\,\mu$ per second, the range being about six times. The construction of this particular apparatus enables the balance to be secured within these limits. The adjusting mechanism consists of a centrifugal governor and a frictional resistance. The two arms of the governor can be increasingly outspread by a right-handed turn of the screw S (see fig. 9). This increases not only the

inertia of the revolving governor, but also the friction of the lower points of the arms of the governor which rub against a horizontal circular plate, not shown in the figure. Increasing inertia and friction both tend to slow down the speed of the rotation of the vertical spindle on which the rate of subsidence of the plant depends. A left-handed turn of the adjusting screw S causes, on the other hand, a continuous increase in the rate of subsidence.

When the adjusting screw has been set at a particular position, the balancing rate of subsidence of the plant remains constant for many hours. The attainment of

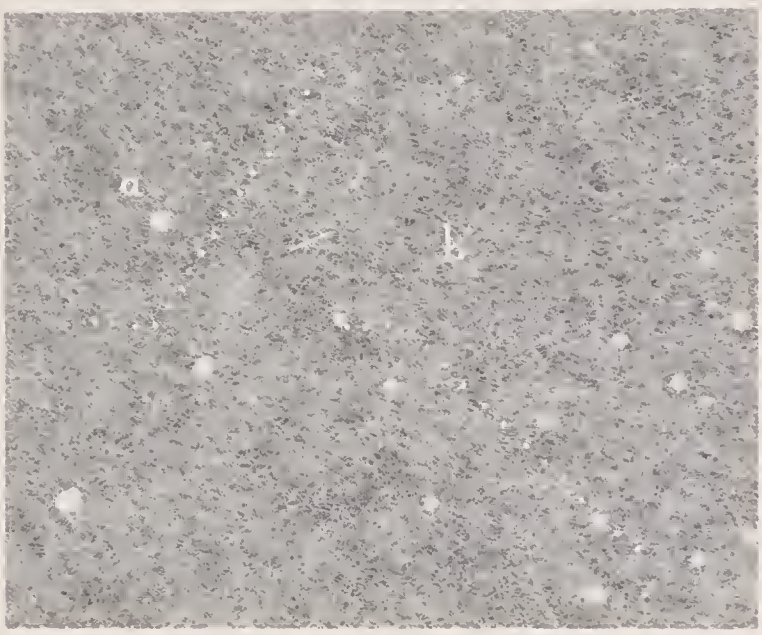


FIG. 10.—Record showing (a) condition of overbalance, and (b) underbalance of growth. (Magnification 2000 times.)

this constancy is a matter of fundamental importance in accurate investigation by this method.

The ease and exactitude of securing the balance are shown in the records (fig. 10, *a* and *b*). In each of these the exact balance is seen in the first part of the record at a definite position of the adjusting screw. A slight turn of the screw to the right reduced the rate of subsidence, resulting in the upset of growth-balance upwards (fig. 10, *a*). A turn of the screw in the opposite direction caused overbalance of the growth-rate, the resulting curve being downwards (fig. 10, *b*).

Calibration.—This is effected as follows: the rate of

subsidence of the plant-holder which balances the rate of growth is, as already stated, proportional to the rate of rotation of the vertical spindle with the dependent train of revolving clock-wheels. A striker is attached to one of the wheels and a bell is struck at each complete revolution. The clockwork is adjusted by the governor to revolve at a medium speed, the bell striking 35 times in a minute. A microscope-micrometer is focused on a mark made on the plant-holder, and the amount of subsidence of the mark is determined during one minute; this was found to be 0·0525 mm. As this fall occurred when the bell was striking 35 times in a minute, the subsidence per stroke was 0·0015 mm. From this it is possible to determine the absolute rate of growth.

Determination of the absolute rate of growth.—Supposing that balance occurred at N strokes of bell per minute, the rate of balancing subsidence $= N \times 0 \cdot 0015$ mm. per minute; $= N \times 0 \cdot 000025$ mm. per second; $= N \times 0 \cdot 025\ \mu$ per second.

Experiment 7.—The growth of a specimen of *Zea Mays* was found to be balanced when the number of strokes of the bell was 20 per minute (absolute rate of growth $= 20 \times 0 \cdot 025\ \mu = 0 \cdot 5\ \mu$ per second); the length thus measured is equal to the wave-length of sodium light. This affords some idea of the sensitiveness of the Crescographic Method of Balance.

Growth-scale.—All necessity for calculation is obviated by the scale attached to the apparatus. The speed of the clockwork which brings about the balance of growth is determined by the position of the adjusting screw S, the gradual lowering of which produces a continuous diminution of speed. A particular position of the screw therefore indicates a definite rate of subsidence for balancing the growth. The up or down movement of the screw causes rotation of an index pivoted at the centre of a circular scale. Each division of the scale is calibrated by counting the corresponding number of strokes of the bell per minute

...tions of the screw. Rates of growth from, say, 0·[illegible] μ to 1·2 μ per second can thus be found directly from the readings of the scale.

The determination of the rate of growth now becomes extremely simple. A few turns of the screw cause an exact balance of growth, the index indicating the absolute rate. The procedure is even simpler and more expeditious than the determination of the weight of a substance by means of a balance.

B. Method of Compensation by an Inclined Plane

With the apparatus already described, it is possible to balance growth within the range of 0·17 μ to 1·[illegible] μ per

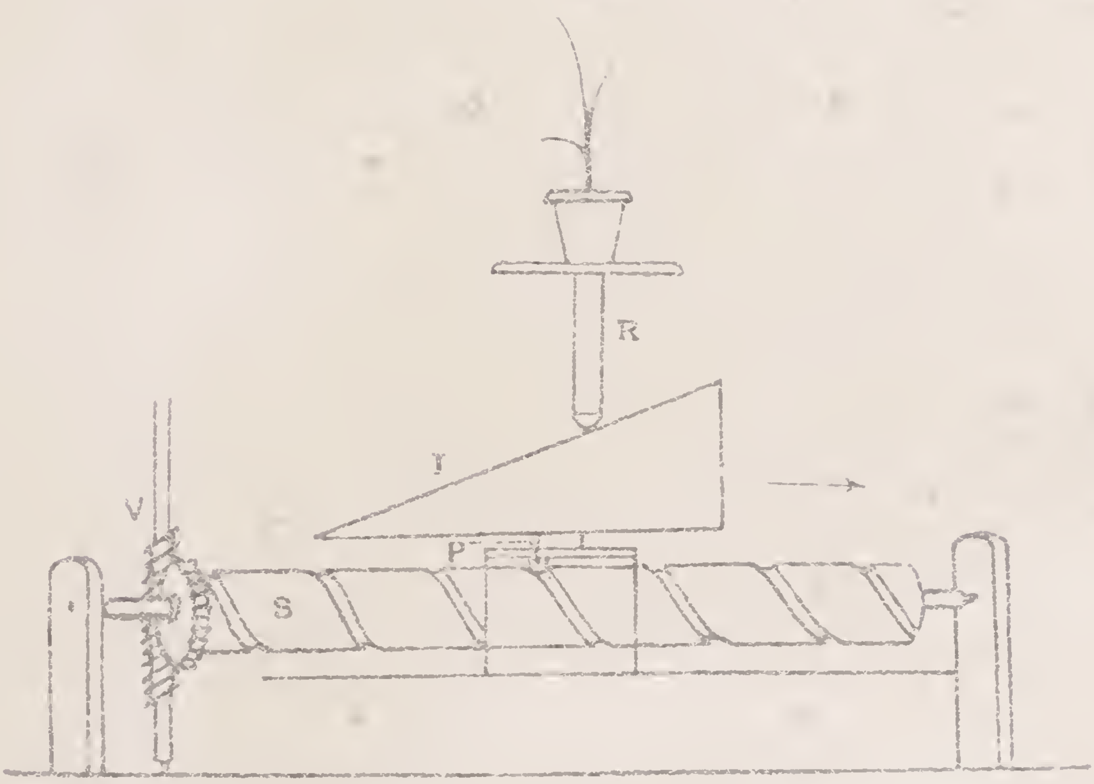


FIG. 11. Diagram of Method of Inclined Plane.

I, inclined plane pushed forward by revolving screw S, at rate adjusted by rotation of vertical spindle V. The lower end of rod R of the plant-holder rests on the inclined plane. (See text.)

second; other instruments have to be employed when the rate of growth is quicker or slower. In order to meet all requirements in a single instrument, it became necessary

to devise a universal apparatus based on a
that of the inclined plane.

Imagine the plant-holder so held that its lower pointed end rests on an inclined plane which slopes down to the left; suppose further that the inclined plane is being pushed forward to the right at a uniform rate. This will result in the gradual subsidence of the plant-holder, the rate depending on the angle of inclination (fig. 11). When the angle is reduced to zero, the plane becomes horizontal, and there is no subsidence, the balancing arrangement being thus put out of operation. The rate of subsidence is, on the other hand, gradually enhanced by a continuous increase in the angle of inclination.

The rate of forward movement of the inclined plane has been assumed to be constant. It is obvious that greater speed of movement of the plane will correspondingly increase the rate of subsidence. The problem of balancing widely different rates of growth was solved by appropriate modifications of the angle of inclination of the plane and the rate of its forward movement. In practice, instead of a solid inclined plane, a board is employed the inclination of which can be varied.

The rate of subsidence for balancing growth will thus depend on the following:

1. On the constant of the particular apparatus;
2. On the angle of inclination; and
3. On the rate of forward movement of the plane as determined by the period of rotation of the vertical spindle.

Taking these factors into consideration the formula for absolute measurement of

$$\text{the rate of growth } \mu \text{ per second} = \frac{K \tan i}{t}.$$

K is the constant of the apparatus;
i is the angle of inclination; and
t is the period of a complete revolution of the vertical spindle in seconds.

The angle of inclination of the plane can be read on the circular scale. The interval between two successive strokes

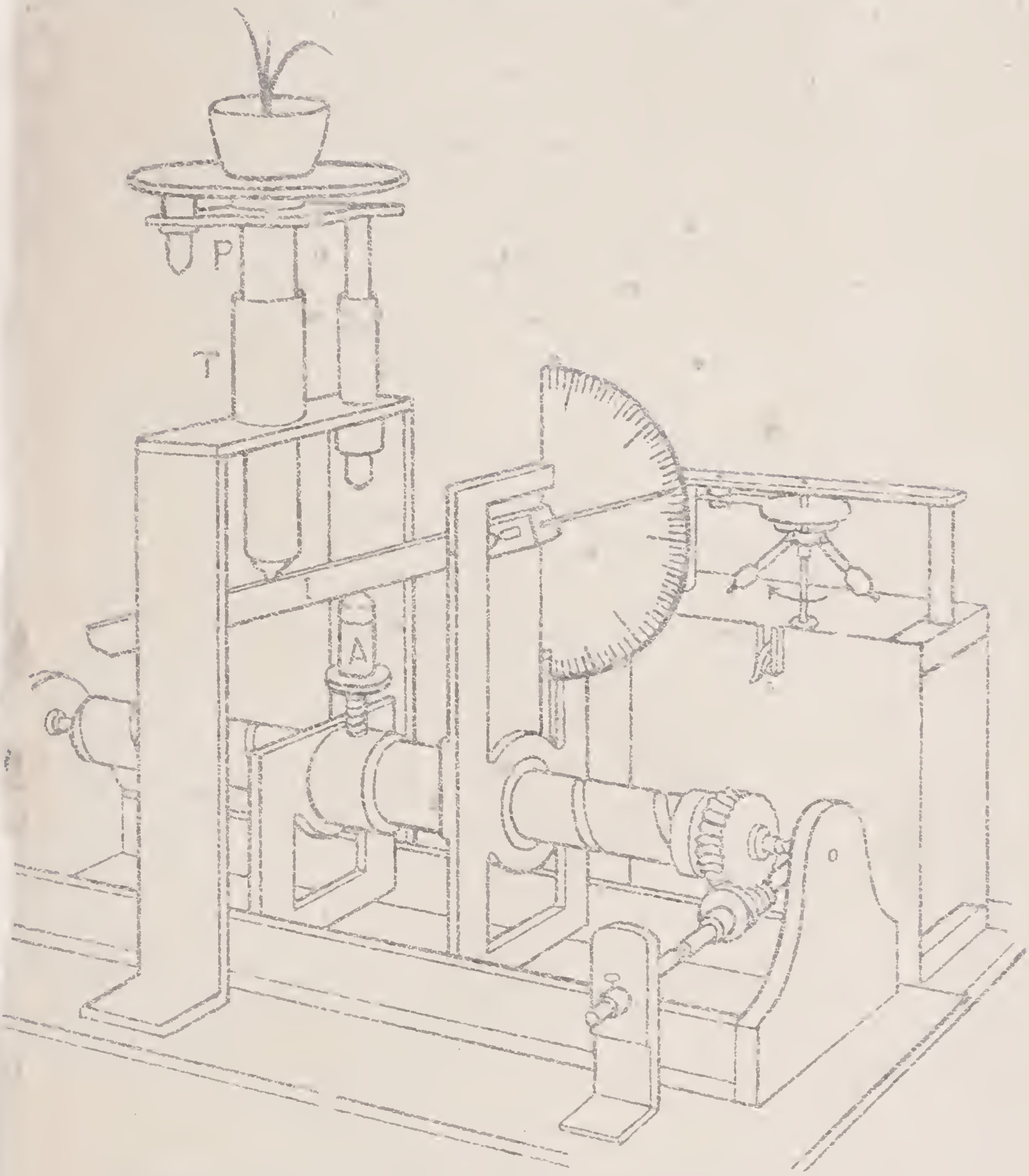


FIG. 12. The complete apparatus for Balance by Inclined Plane.

A, screw for adjustment of angle of inclination of plane, read in circular scale; P, rod supporting plant holder enclosed in watch tube T.

of a bell gives the period of a complete revolution of the vertical spindle.

A photographic reproduction of the complete balancing apparatus, reduced one-third, is given in fig. 12.

Experimental Verification of the Formula

Experiment 8.—The reliability of the apparatus and the accuracy of the working formula were tested by independent measurements obtained (1) by the method of balance, and (2) by direct micrometric measurement of growth of a seedling of Wheat.

Measurement by the Balance Method :

The constant of the apparatus = 10·45.
The balancing angle of inclination = 23·5°.
The time of a single revolution of spindle = 12 seconds.

Hence absolute rate of growth in μ per second

$$= \frac{10 \cdot 45 \times \tan 23 \cdot 5^\circ}{12}$$

$$= 0 \cdot 381 \quad . \quad . \quad . \quad . \quad . \quad (1)$$

Direct measurement by Microscope-Micrometer.—The micrometer was focused on a mark on the tip of the plant, and the growth-elongation after an interval of 2 hours and 35 minutes (155 seconds) was found to be 3·5 mm.

The rate of growth μ per second

$$= \frac{3 \cdot 5 \times 1000}{155 \times 60}$$

$$= 0 \cdot 376 \quad . \quad . \quad . \quad . \quad . \quad (2)$$

The two results are practically the same, the difference being in the third place of decimals.

The Time-Factor

The factor of time is a very important element in the responsive growth-variation. Growth is not immediately affected by an external change; there is a delay in the reaction, designated as the *latent period*; this has to be accurately determined, as also its modification under different

conditions. The effect induced by an external agent is, however, modified by the duration of its influence. The intensity of the reaction may thus increase at the first, reach a climax and then undergo an actual decline. No method had hitherto been available for immediate detection and record of these changes, moment after

FIG. 13. Record showing the effect of Carbonic Acid Gas on growth.

Horizontal line at the beginning indicates balanced growth. Application of carbonic acid gas induces preliminary enhancement of growth, shown here by up-curve. The growth-rate becomes normal for a while with subsequent depression, shown by down curve. Successive dots at intervals of 10 seconds. (Wheat.)

moment, as they occur. The Method of Balance offers, in this respect, unique advantages.

The following are the characteristics of the curves obtained by the balancing method. The initial horizontal record indicates balance of the normal rate of growth. The delay in the responsive variation is the latent period; the up-curve represents enhancement of the rate of growth. [illegible]

of the experiment the curve becomes once more horizontal it indicates the resumption of the normal rate. The following results give a striking demonstration of the influence of the time-factor.

Experiment 9. *Effect of Carbonic Acid Gas on growth.*—After obtaining the balance of growth with a seedling of Wheat, the plant-chamber was filled with CO_2 diluted with air, the moment of application being marked with an arrow in the record. There was an almost immediate acceleration of the rate of growth, the latent period being less than 5 seconds. This enhanced rate continued for 120 seconds, slowing down gradually to the normal and remaining so for 20 seconds as indicated by the horizo record at the top of the curve. Continued action of induced, however, an inversion of the curve, the d record indicating a rate below the normal (fig. 13). Str of dose exerts its characteristic influence, very dilute inducing acceleration, while stronger concentration or lo application of the gas brings about a quick rev from acceleration to retardation, culminating in arres growth.

Two different methods are thus available for inv gations on growth; the ordinary Method of Crescograph Magnification, and the excessively sensitive Method of Balance. The results obtained by the second method will be found not merely to confirm those obtained by the first, but also to afford important information regarding the influence of the time-factor in its relation to growth.

Summary

In the Method of Balance the upward movement of growth is compensated by a corresponding subsidence of the plant. Two different methods of balance have been successfully employed: (1) that of the Falling Weight, and (2) that of the Inclined Plane.

In the condition of balance, the record remains horizontal.

The effect of an external agent is quickly detected by the upsetting of the balance, upwards or downwards. An up-curve represents acceleration above, and a down-curve depression below, the normal rate.

The influence of the time-factor is shown in the changing flexures of the record.

CHAPTER IV

EFFECT OF VARIATION OF TEMPERATURE ON GROWTH

ACCURATE determination of the effect of temperature on growth presents many difficulties due to the presence of the numerous complicating factors. In order to reduce these to a minimum, it is advisable to carry out the experiment with an identical plant, observing its rate of growth at different temperatures. The period of the experiment should, moreover, be as short as possible, so as to eliminate the complication which arises from the diurnal variation of the rate of growth. A quick change of the temperature of the plant-chamber is therefore necessary, which unfortunately introduces unexpected difficulties; for a rapid change of temperature acts as an excitatory shock, inducing contraction of the growing organ. This drawback can be obviated to a great extent by securing a *gradual* instead of an abrupt variation of temperature. The temperature of the plant-chamber has, therefore, to be gradually raised or lowered. This has been secured in the following manner: a cylinder of thin metal with its base closed serves as the plant-chamber P, kept in a humid condition by a piece of moist sponge (fig. 14). The cylinder P is enclosed in a larger vessel T.R. filled with water and serving as the thermal regulator. There are two reservoirs, H and C, containing hot and ice-cold water respectively. Opening of the stopcocks S_1 and S_3 allows hot water to stream through the thermal regulator, the excess escaping through the outflow pipe O. The opening of S_2 and S_3 allows, on the other hand, a stream of cold water to flow through the

thermal regulator. The rate of heating or cooling of the regulator depends on the rate of inflow of hot or cold water. To effect a gradual rise of temperature in the plant-chamber the stopcock S_1 is first opened. The experimenter, keeping his hand on the stopcock S_3, then carefully adjusts the rate of inflow; he has before him a clock-hand which goes round once in a minute, and with previous practice he is able to adjust the inflow, so that the rate of rise of temperature of the plant-chamber, indicated by the thermometer T,

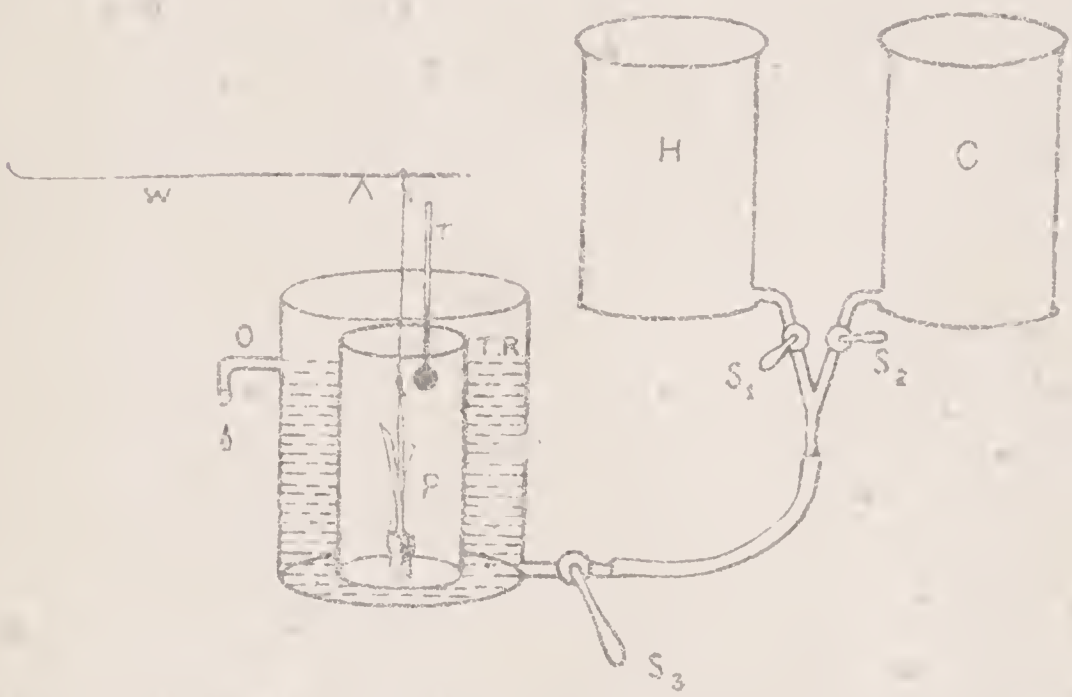


FIG. 14. Arrangement for variation of temperature of plant-chamber.

P, plant-chamber enclosed in thermal regulator T.R. H and C, reservoirs containing hot and cold water. Variation of temperature of thermal regulator adjusted by proper manipulation of stopcocks S_1, S_3, and S_2, S_3. O, outflow pipe. Plant attached to recording lever W. T, thermometer.

is half a degree every 30 seconds or one degree every minute. The mass of water in the thermal regulator acts as a stabiliser, preventing any sudden fluctuation of temperature. A similar method is also employed for the gradual lowering of temperature. The adoption of this device for ensuring gradual variation of temperature was found to eliminate the erratic changes in the rate of growth which had previously proved to be so extremely baffling.

METHOD OF DISCONTINUOUS OBSERVATION

Determination of cardinal points of temperature.—The cardinal points are not the same for different plants: even in the same species they are modified by the climate to which the plants have been habituated. The results obtained in the tropics must necessarily be different from those in colder climates. The following experiments were

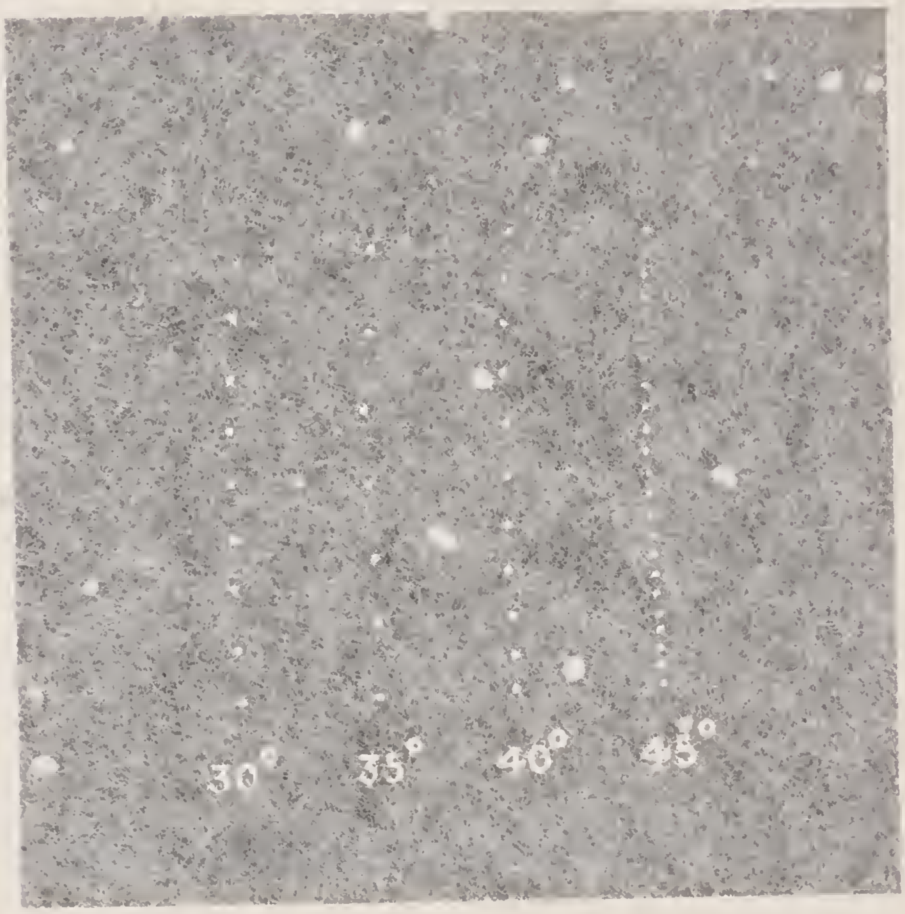


FIG. 15. Records of growth, on stationary plate, at different temperatures.

carried out in Calcutta in the spring season, when the average temperature is about 30° C.

Experiment 10. *The optimum temperature.*—High magnification records of the growth of Kysoor were taken on a stationary plate for selected temperatures of 30°, 35°, 40°, and 45° C., each of these being kept constant during the period of observation. The records (fig. 15) show that the rate of growth increases with the rise of temperature to an optimum, above which the rate undergoes depression. In the different records given in the figure, the time-interval

between the successive dots is the same; but for completing the same length of growth elongation the number of dot-intervals is different. At 30° C. it is eight, at 35° it is six, at 40° it is ten, and at 45° it is twenty two. The rate of growth at 35° is thus nearly one and a half times that at 30°; at 45°, on the other hand, the rate has fallen to nearly a third. In some cases there was no growth even at 40°, when pulsations were exhibited in each of which the up- and down-curves are nearly equal.

For Kysoor the optimum temperature is about 35°, but there are plants in which the optimum is as low as 28°, and continues for about the next eight degrees.

Experiment 11. *The temperature minimum.*—The experiment was carried out with Kysoor subjected to a continuous lowering of temperature by adjusting a flow of ice-cold water into the thermal regulator. It was found that the rate of growth underwent continuous depression, till arrest took place at 22° C. The temperature was then gradually raised, growth being feebly revived at 23°. The minimum temperature may therefore be regarded as 22·5° C.

Experiment 12. *Effect of higher temperatures.*—Growth was found to be greatly retarded at 55°; at 60° there occurred a sudden spasmodic contraction, which I have shown elsewhere to be the spasm of death.[1] This spasmodic death-contraction is the immediate effect of the fatal temperature. Prolonged exposure to a temperature a few degrees below 60° would no doubt be followed by the death of the organ.

METHOD OF CONTINUOUS OBSERVATION

The above method of observation, though not ideally perfect, was fairly satisfactory: a minor defect was, however, discovered as the result of further observation. The plant, according to the method described, was surrounded by

[1] *Plant Response* (1906), p. 118; *Comparative Electro-Physiology* (1907), pp. 302–316.

air which is a bad conductor of heat. The plant could not, therefore, quickly assume the temperature of the outside regulator. In the method of continuous observation which was contemplated, it was essential that the temperature of the plant itself should undergo continuous and rapid change.

An additional difficulty arose from the radiation of rays of heat from the sides of the thermal regulator, which induces retardation of growth. The enhancement of the rate of growth by rise of temperature is thus antagonised by the effect of radiation. The difficulties arising from the non-conductivity of the air and from thermal radiation were removed by filling the inner plant-chamber with water, which is a better medium for transport of heat. Further experiments showed that the plant quickly assumed the temperature of the water in which it was immersed, provided that the thermal rise was at a uniform rate of, say, 1° C. per minute. Heat being conveyed by the water, the disturbing effect of radiation was eliminated.

The elongation recorded by the Crescograph during rise of temperature may be due (1) to physical expansion, (2) to expansion resulting from absorption of water by the plant, and (3) to an enhanced rate of growth. The relative values of the first two factors in comparison with growth-elongation were found by carrying out parallel experiments with two different specimens, in one of which growth had already been completed whilst in the other it was still in full activity. Records of the two specimens were taken under the same magnification for a rise of 20° C. In order to keep the record of the actively growing organ within the plate, the magnification had to be reduced to 250 times. The joint effects of thermal expansion and absorption of water in the non-growing plant gave an elongation of only 1 mm.; whereas, under similar circumstances, the elongation of the actively growing plant was more than 100 mm. Compared with the physiological reaction, the physical effects were quite negligible.

THE THERMOCRESCENT CURVE

I was desirous of devising a method by which an automatic and continuous curve could be obtained recording the rate of growth between 22° and 40° C. The entire record had to be completed within the short period of 18 minutes, at a rate of rise of temperature of 1° C. per minute. Previous experiments, as already stated, showed

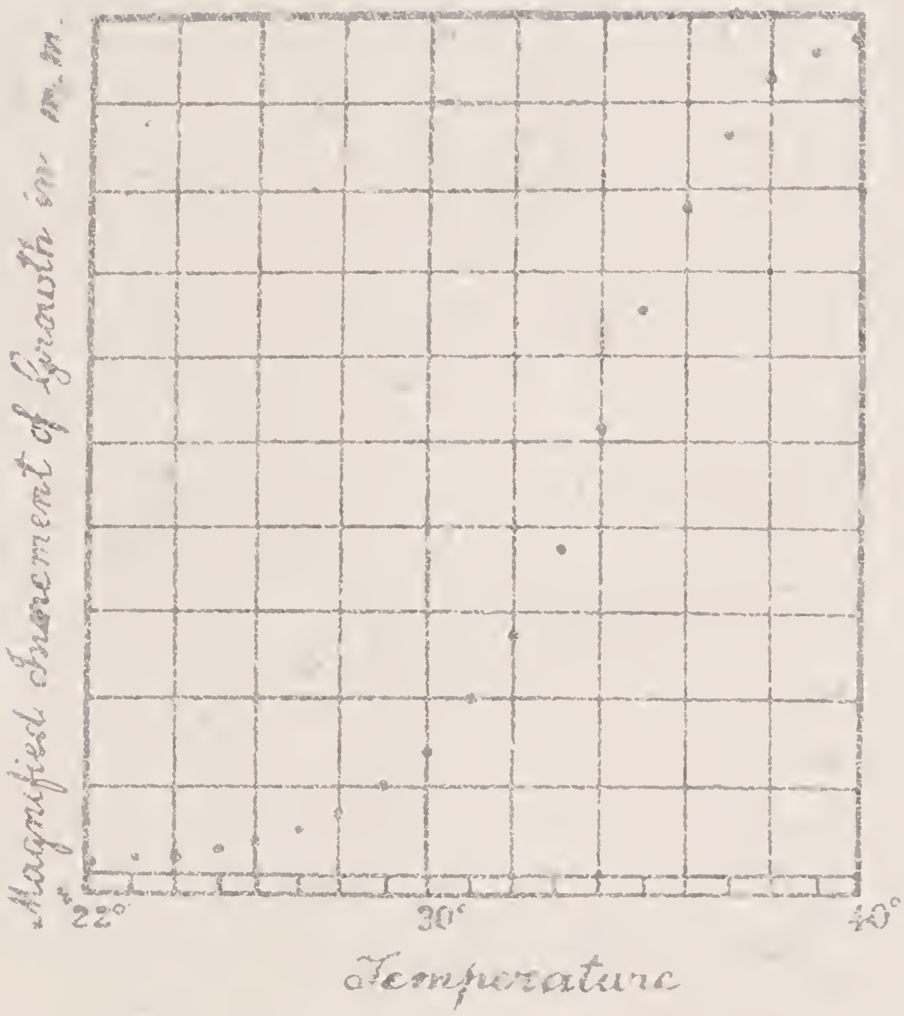


FIG. 16. The Thermocrescent Curve.
Ordinate represents increment of growth; abscissa, increment of temperature.

that at this rate of *continuous* rise of temperature there is practically no lag in the plant assuming the temperature of the bath, especially when it is a thin specimen.

Experiment 13.—The specimen employed was Kysoor, in which arrest of growth occurred at the minimum temperature of 22° C. The temperature was now raised at the uniform rate of 1° C. per minute. The curve of growth was taken on a moving plate which travelled at the rate of

5 mm. per minute. The recording lever inscribed successive dots at intervals of a minute, during which the temperature rose 1°. A THERMOCRESCENT CURVE was thus obtained, the ordinate representing increment of growth, and the abscissa the time as well as the rise of temperature. The curve (fig. 16) shows growth at standstill at 22° C. The growth was at first slowly increased with the rise of temperature, and then more quickly. At 33° C. the rate of increase of growth was very rapid, attaining its maximum at or about 34° C. At higher temperatures the rate underwent a rapid decline, being reduced at 39° C. to about a fifth of the optimum rate.

Determination of absolute rate of growth at different temperatures.—The THERMOCRESCENT CURVE (*see* fig. 16) gives sufficient data for the calculation of absolute rates of growth at different temperatures. The vertical distance between successive dots is the increment of growth in 1 minute for a rise of 1° of temperature between T and T′. If l represents the magnified growth-elongation in millimetres for a period of 60 seconds, and m the magnifying power of the recorder, then the absolute rate of growth for the mean temperature $\frac{T + T'}{2}$ is found from the formula:

$$\text{Absolute rate of growth at } \frac{T + T'}{2} = \frac{l \times 10^3}{m \times 60}\ \mu \text{ per second.}$$

The results thus calculated are given below in a tabulated form.

TABLE II.—RATE OF GROWTH FOR DIFFERENT TEMPERATURES (KYSOOR).

Temperature	Growth	Temperature	Growth
22° C.	0·00 μ per sec.	31° C.	0·45 μ per sec.
23° C.	0·02 μ ,,	32° C.	0·60 μ ,,
24° C.	0·04 μ ,,	33° C.	0·80 μ ,,
25° C.	0·06 μ ,,	34° C.	0·92 μ ,,
26° C.	0·08 μ ,,	35° C.	0·84 μ ,,
27° C.	0·12 μ ,,	36° C.	0·64 μ ,,
28° C.	0·16 μ ,,	37° C.	0·45 μ ,,
29° C.	0·22 μ ,,	38° C.	0·30 μ ,,
30° C.	0·32 μ ,,	39° C.	0·16 μ ,,

I give below a curve (fig. 17) constructed from the above data, showing the relation between temperature and rate of growth.

The methods described possess important advantages. In place of measuring the average change in the rate of growth in a number of plants, the variation is recorded in an identical specimen. The employment of magnification reduces, moreover, the period of the whole experiment to

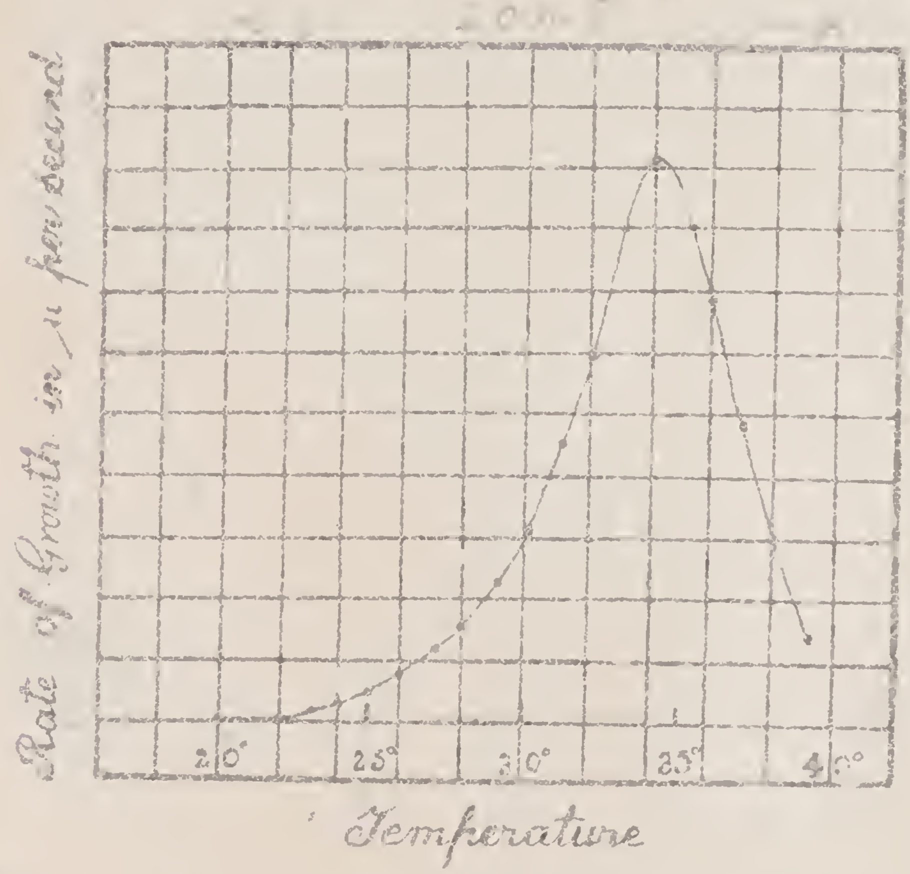


FIG. 17. Curve showing relation between temperature and rate of growth.

about 20 minutes, and thus eliminates the complication arising from the diurnal variation in the rate of growth.

SUMMARY

Methods of experimentation have been described for rapid determination of the effect of variation of temperature on the rate of growth.

Radiant heat induces a retardation of growth which antagonises the acceleration due to rise of temperature; the gradual rise of temperature of the plant has therefore

to be so effected as to eliminate this source of error. A continuous record of growth under uniform rise of temperature gives a THERMOCRESCENT CURVE, from which the absolute rate of growth at different temperatures can be found.

Different plants exhibit characteristic differences in their cardinal points of temperature. In the tropical plant Kysoor the minimum temperature for arrest of growth is 22·5° C., the optimum is about 34° C. The growth-rate declines as the temperature rises further, and becomes arrested at or about 55° C. A sudden spasmodic death-contraction occurs at 60° C.

CHAPTER V

THE EFFECT OF CHEMICAL AGENTS ON GROWTH

THE record of the effect of chemical agents on growth may be taken on either a stationary or a moving plate. The method of application is as follows: for the study of the action of gases and vapours, the plant is enclosed in a cylindrical chamber constructed of a sheet of mica provided with inlet and outlet pipes for circulation of different gases and vapours, the chamber being maintained in a humid condition by pieces of sponge soaked in water. In the case of liquid chemical agents, the specimen is suitably mounted in a glass cylinder filled with water, and the normal rate of growth recorded. This remains constant for about an hour, in the course of which the experiment should be concluded, as prolonged deprivation of oxygen affects the growth of the plant. After taking the normal record, the chemicals are added to the water, and the strength of solution gradually increased. The chemical agents may be broadly divided into three classes: (1) stimulants; (2) anaesthetics; and (3) poisons.

EFFECT OF STIMULANTS

Experiment 14. *Hydrogen Peroxide.*—A 1 per cent. solution of this agent was often found to enhance the rate of growth: in some cases the enhancement was as much as two and a half times the normal rate.

EFFECT OF ANAESTHETICS

The results given below indicate that Carbonic Acid Gas, Ether, and Chloroform act as mild or strong anaesthetics in the above order.

Effect of Carbonic Acid Gas

Experiment 15.—The immediate effect is a very marked acceleration of growth. With a seedling of Onion (Allium) the increase was found to be two and a half times. With the flower-bud of Crinum the rate was enhanced threefold, from the normal 0·25 μ to 0·75 μ per second. After the preliminary enhancement, there was a depression of growth within 15 minutes of the application, the rate being now reduced to 0·15 μ per second (fig. 18). These effects taking place equally in light and darkness prove that the phenomenon is independent of photosynthesis. The immediate and subsequent effects of CO_2 on growth have already been demonstrated by the highly sensitive method of balance (*cf.* fig. 13).

FIG. 18. Effect of Carbonic Acid Gas on growth.
a, normal rate; *b*, enhanced rate as the immediate effect; *c*, retarded rate after prolonged application (Crinum).

Effect of Vapour of Ether

The following may serve as typical examples of results obtained with various plants. Among these may be mentioned the seedlings of Wheat; stems of Helianthus and of Dahlia; petiole of Tropaeolum; tendril of Cucurbita; peduncles of Hibiscus, Centaurea, Daffodil, and of Allium; the flower-bud of Crinum Lily and the pistil of Datura. The effects observed were essentially similar in all cases, of which three representative examples will be described in detail.

Experiment 16. *Seedling of Wheat.*—The specimen was an intact seedling with roots; it exhibited a fairly rapid rate of growth, as shown in the first part of the record. On

application of ether the growth-rate became very greatly enhanced in less than 15 seconds and this persisted for a considerable length of time, as shown by the erection of the curve and wider spacings between the successive dots (fig. 19, *a*). Prolonged application of ether, however,

FIG. 19. Effect of vapour of ether on growth.

a enhancement of the rate (Wheat seedling); *b*, enhancement followed by depression (Crinum); *c*, renewal of growth of stem in a state of standstill (Helianthus).

subsequently caused a depression of the rate, not shown in the record.

Experiment 17. *Crinum Lily.*—The result was similar to that obtained with the seedling of Wheat. The acceleration occurred within 30 seconds of the application of ether vapour; the enhanced rate persisted for a period of more than 2 minutes, after which the depressing effect of prolonged application is shown, the response curve (fig. 19, *b*) tending to become horizontal.

Experiment 18. *Stem of Helianthus.*—As the cut

specimen was in a state of arrested growth, the effect of application of ether is of much interest. The record (fig. 19, *c*) shows that ether *brought about a renewal of growth previously in a state of standstill.* This renewal occurred after an application of several minutes, the growth persisting for a long time.

Effect of Chloroform

Experiment 19. *Petiole of Tropaeolum.*—The typical effects of chloroform on growth in different organs are given below. The preliminary effect of chloroform vapour, like that of other anaesthetics, is an acceleration of the rate of growth. With the petiole of Tropaeolum this occurred in less than 2 minutes and persisted for a period of 90 seconds. After a further period of 45 seconds growth became arrested; subsequently there was an abrupt contraction due to death-spasm (fig. 20, *a*).

Experiment 20. *Peduncle of Centaurea.*—The specimen was in a state of arrested growth; application of chloroform vapour induced a vigorous renewal of growth in the course of 30 seconds. The renewal of growth occurred under a small dose of the anaesthetic which persisted for 3 minutes, after which there was an arrest followed by the spasmodic death-contraction (fig. 20, *b*).

Experiment 21. *Crinum Lily.*—The specimen in this case was also in a state of arrested growth. Application of chloroform renewed the growth in less than 30 seconds (fig. 20, *c*). Under the continued action of chloroform the revived growth, which had persisted for 2 minutes and 15 seconds, was arrested; this was followed by a violent spasmodic death-contraction.

Experiment 22. *Pistil of Datura.*—The effect of chloroform on normal growth was a great enhancement which occurred in the course of 30 seconds (fig. 20, *d*). This persisted for nearly 2 minutes, after which there was an arrest and subsequent spasmodic death-contraction.

Under chloroform a growing organ thus exhibits a preliminary acceleration of growth followed by contraction, which may be either feeble or very intense. The contraction by itself should not be regarded as the sign of death, for there are agents which induce a temporary contraction from which a revival is possible. The test of the death-spasm is that it is an irreversible change, from which the plant cannot be revived by substituting fresh air

FIG. 20. Effect of vapour of Chloroform.

a, preliminary acceleration followed by arrest and death-spasm (Tropaeolum); *b*, revival of growth (Centaurea); *c*, revival of growth, arrest, and death-spasm (Crinum); *d*, enhancement, arrest, and death-spasm (Datura).

for the anaesthetic. The contraction under the prolonged action of chloroform (by which even the interior of the organ becomes affected) may be taken as the death-spasm, since fresh air fails to revive the plant. Another interesting phenomenon observed after chloroforming the plant is the profuse deposit of minute drops of liquid on the surface. This is due to the forcing out of the sap during death-contraction, the escape being facilitated by the increased permeability of the cell-protoplasm. Dark spots of discoloration soon begin to appear and spread

rapidly over the surface, and the organ exhibits rapid wilting.

It is instructive to compare the death-spasm under an anaesthetic with the parallel effect of stimulation by a strong electric shock. The plant recovers from moderate stimulation and responds again to fresh stimulation. But under excessive stimulation, such as that induced by strong electric shocks, the excitatory contraction passes from a reversible to an irreversible condition associated with death. Both pulvinated and growing organs exhibit a violent contraction from which there is no recovery. In the case of anaesthetics likewise, a mild dose induces a contraction, recovery taking place after substitution of fresh air. But under a stronger dose the violent contractile spasm proves to be the spasm of death.

Effect of Poisonous Agents

This refers to gases or liquids which cause depression and subsequent death of the plant.

Sulphuretted Hydrogen

Experiment 23.—This gas not only exerts a great depressing effect, but is also toxic in its action, which accounts for the impossibility of growing many plants in a town, the air of which contains traces of this gas. For example, *Biophytum sensitivum*, which flourishes and maintains its high sensitivity seven miles out of Calcutta in the suburban area, soon succumbs when brought within the town. The record (fig. 21) shows the marked retardation of growth when the plant is exposed to H_2S even for 15 minutes. In the present case the growth-rate was reduced to half.

Experiment 24. *Ammonium Sulphide*.—This reagent in dilute solution retards growth, and in stronger and long-continued dose acts as a poison. The following results

with a Wheat-seedling were immediately obtained under different strengths of solution :

Normal rate	0·30 μ per second
0·5 per cent. solution . .	0·15 μ ,, ,,
2·0 ,, ,, . .	0·08 μ ,, ,,

Copper Sulphate Solution

Experiment 25.—A minute dose of copper sulphate solution of about 0·1 per cent. was found to induce

Fig. 21.

Fig. 22.

Fig. 21. Effect of Sulphuretted Hydrogen (Wheat-seedling).
Fig. 22. Effect of Copper Sulphate solution.

immediate enhancement of the rate of growth, whereas a stronger dose of 5 per cent. caused depression of the rate (fig. 22), a remarkable instance of a minute dose of poison acting as a stimulant. The following data relate to the effect of 1 per cent. $CuSO_4$ solution on the rate of growth. The normal rate of growth of a Wheat-seedling was 0·45 μ per second ; application of 1 per cent. solution reduced the rate to 0·13 μ per second. Long-continued action of the solution caused the death of the plant.

SUMMARY

The effect of a chemical agent on growth is determined by the strength of the dose, the duration of application, and the tonic condition of the tissue. A poisonous substance in minute doses often has the effect of enhancing the rate of growth.

The effect of any chemical agent on various growing organs, such as the stem, the petiole, the flower-bud, and the pistil, is essentially the same.

The various anaesthetics induce more or less similar reactions on growth; of these carbonic acid gas may be regarded as a mild and chloroform as a strong anaesthetic.

Carbon dioxide induces a preliminary enhancement of the rate of growth; its continued action is followed by decline and arrest of growth. The influence of CO_2 is the same in darkness as in light, the effect being thus independent of photosynthesis.

A small dose of ether induces a great enhancement in the rate of growth; a large dose paralyses growth, but timely substitution of fresh air is followed by revival.

The effect of continued action of chloroform vapour on growth is as follows: at the first stage there is acceleration; at the second stage growth becomes arrested; at the third stage there is a violent contraction which is the spasm of death.

A small dose of ether or chloroform renews growth which had previously been in a state of standstill. This no doubt explains the action of these anaesthetics in forcing growth of dormant buds in winter.

Sulphuretted hydrogen retards growth and acts as a poison; the effect of ammonium sulphide is similar.

Copper sulphate, in minute doses, often has the effect of enhancing the rate of growth. A stronger dose, or a prolonged action, however, induces a depression which culminates in the death of the plant.

CHAPTER VI

RELATION OF TURGOR AND OF TENSION TO GROWTH

An important condition for growth is the supply of water to the growing region, so that the cells may be in a turgid state. The favourable condition of turgor can only be assured by the pumping up of water from the soil, growth being thus dependent upon the ascent of sap. I will first describe the effects induced in growth by changes in the rate of ascent of sap.

Growth Revived after Irrigation

Experiment 26. *Growth-arrest and revival.*—The experiment was carried out with a seedling of Cucurbita 12 cm. in height, growing in a small pot. Under excessive drought the growth of the plant had been brought to a state of standstill. The stem was held at its lower end in a clamp and 2 c.c. of water was supplied to the root, growth becoming revived after a latent period of 11 seconds. This delay was due to the time taken for the water to reach the growing region, and to impart sufficient turgidity to the cells for the initiation of growth. It was interesting to find the growth-record exhibiting pulsations (*see* fig. 23). The small quantity of water supplied was sufficient to maintain growth for only 3 minutes, after which it came to a standstill. Another 2 c.c. of water was next applied, resulting in a renewal of growth for about 4 minutes or so; the latent period was, however, considerably reduced. The shortening

of the latent period was due to the fact that on the second occasion there was less loss of time in getting the cells sufficiently turgid for the renewal of growth. The response of growth thus followed for a time after each doling out of water.

Experiment 27.—A similar result was obtained with a seedling of *Vicia Faba*, the growth of which, on account of drought, was in a state of standstill. Application of a small quantity of water produced a short-lived revival of growth, which occurred in a pulsatory manner (fig. 23). A second application produced a similar revival, the amplitude and frequency of pulsation being quicker than in the last case. Application of a larger quantity of water produced a persistent revival of growth, the constituent pulsations of which followed each other with such rapidity that it appeared to be continuous.

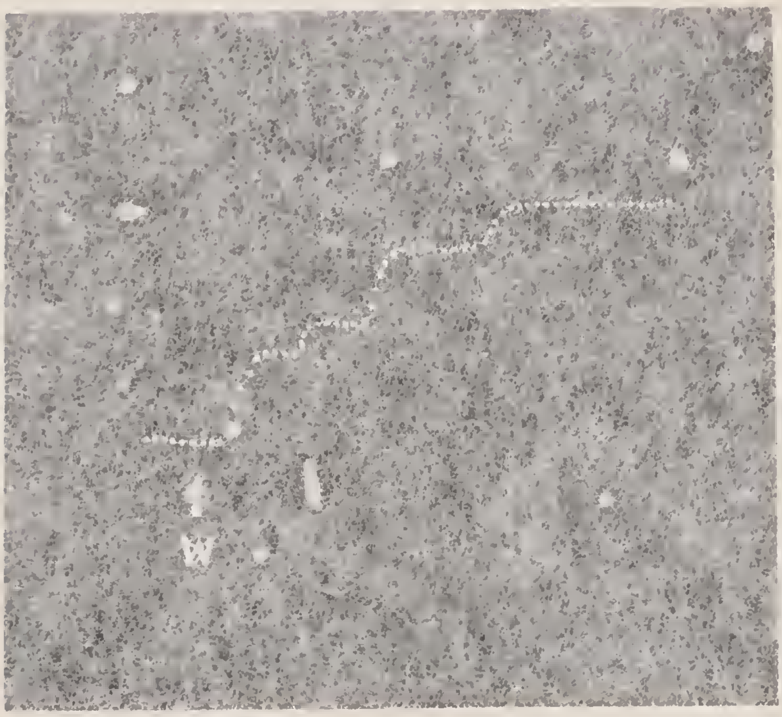


FIG. 23. Growth at standstill revived after irrigation with water.

A small quantity of water revived growth for a short time. Note pulsation of growth. (Vicia Faba.)

EFFECT ON GROWTH OF VARIATION OF ASCENT OF SAP

I have shown elsewhere that the rate of ascent of sap is increased when warm water is used for irrigation, and decreased when cold water is used for the same purpose. Since activity of growth is normally dependent on the ascent of sap, the rate of growth may be expected to be appropriately modified by irrigation with either warm or cold water.

Experiment 28. *Effect of irrigation with cold and with warm water.*—A specimen of Kysoor with a quantity of soil surrounding the root (enclosed in a small bag) was employed for this experiment. The lower part of the plant was securely fixed on a stand, the tip being attached to the Crescograph. The specimen was then subjected to partial drought, water being withheld for a day. This caused a depressed rate of growth, but not complete arrest. The record D (fig. 24) exhibits the depressed rate of growth under partial drought. Cold water was then applied to the root and the effect is shown in record C. Finally, the record H was obtained after irrigation with warm water. It will be seen that the spacings between successive dots at intervals of 10 seconds in the three records are very different. While a given growth-elongation under drought took place in 19 × 10 seconds, a similar lengthening occurred after irrigation with cold water in 13 × 10 seconds, and after irrigation with warm water in 3 × 10 seconds. Enhancement of the rate of ascent of sap by irrigation with warm water is thus seen to have increased the rate of growth more than six times (fig. 24).

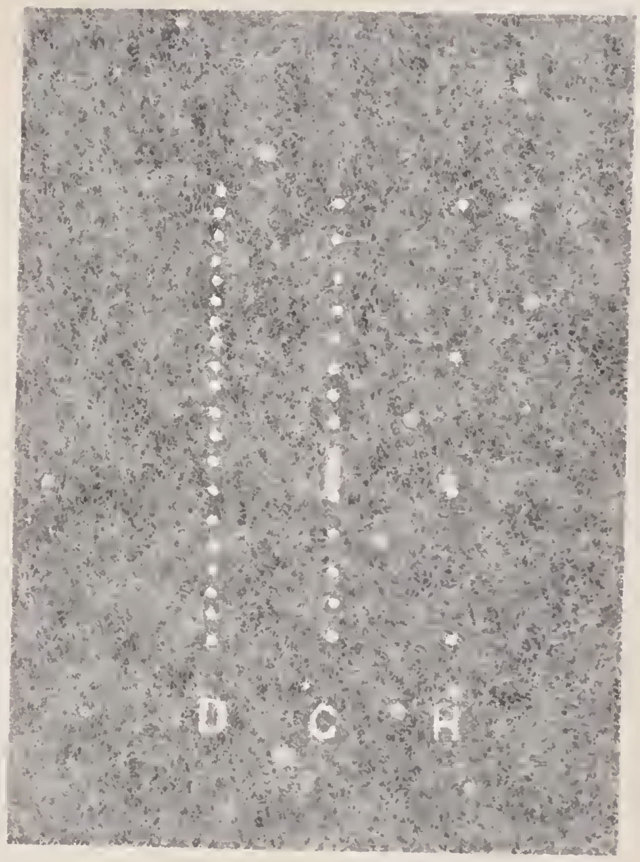


FIG. 24. Effect of irrigation on growth.

D, record of growth under partial drought; C, acceleration after irrigation with cold water; H, enhanced acceleration of growth after irrigation with warm water (S. Kysoor).

The interval between irrigation and responsive variation of growth will obviously depend (1) on the intervening distance between the root and the region of growth, and (2) on the vital activity underlying the ascent of sap. This activity is increased by the action of warm water. In the

case described, the increased rate of growth on irrigation with cold water took place after 70 seconds; but the responsive growth-elongation after application of warm water occurred in less than 20 seconds.

In regard to the effect of irrigation with warm water, certain precautions have to be taken, for sudden application of hot water is liable to induce excitatory contraction. it is therefore advisable to commence irrigation with tepid and end with warm water. The transport of warm water to the growing region may, however, introduce a complication of enhancement of growth by the rise of temperature. This uncertainty may be obviated by waiting for the tissue to return to the temperature of the room. The persistent rate of growth may then be regarded as solely due to the enhanced activity of the ascent of sap.

Experiment 29. *Temporary and persistent enhancement of growth.*—The results obtained with the peduncle of Zephyranthes will be found to be of interest in this connection. Its rate of growth under partial drought was found to be 0·04 μ per second; application of warm water increased the rate to 0·20 μ per second. After 15 minutes the rate fell to 0·13 μ, and after an hour to the permanent rate of 0·08 μ per second. It will be noted that even then it was twice the initial rate before irrigation.

I give below a table which shows the immediate effect on growth of irrigation with cold and with warm water, the persistent effect being given in Table IV:

TABLE III.—EFFECT OF IRRIGATION WITH COLD AND WITH WARM WATER.

Specimen	Condition of experiment	Rate of growth
Kysoor .	Dry soil	0·21 μ per sec.
	Irrigation with cold water	0·30 μ ,,
	Irrigation with warm water	1·33 μ ,,
Peduncle of Zephyranthes	Dry soil	0·04 μ ,,
	Irrigation with warm water	0·20 μ ,,

Effect of Positive and Negative Variation of Turgor

The acceleration of growth by the enhancement of turgor caused by increased rate of ascent of water having been demonstrated by the last experiment, I then proceeded to observe the effect of diminution of turgor in the very same organ.

Experiment 30. *Effect of alternate supply and withdrawal of water.*—The rate of growth of the peduncle of Zephyranthes in the condition of partial drought was, as already stated, 0·04 μ per second, increased to 0·20 μ after irrigation with warm water. The permanent rate of growth after irrigation was found to be 0·08 μ per second. A strong solution of KNO_3 was then applied to the root in order to withdraw water, with the result that the rate of growth quickly declined to 0·03 μ per second, being nearly one-third the previous rate (fig. 25). The induced depression was thus greater than that under condition of drought. The table shown on page 56 is a statement of the results.

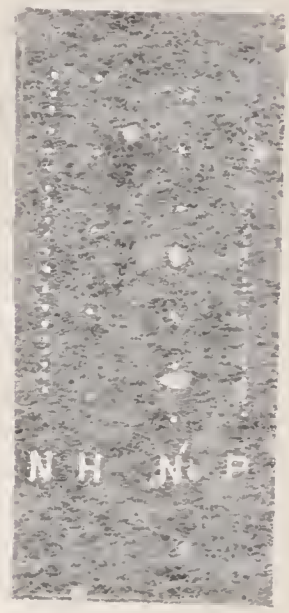


FIG. 25. The effects of alternate application and withdrawal of water on growth

N, normal rate under drought; H, enhanced rate after irrigation with warm water; N', subsequent permanent rate; P, diminished rate of growth after plasmolytic withdrawal of water (Zephyranthes).

The results given show that the rate of growth is enhanced, within limits, by an increase of turgor due to more rapid supply of water; withdrawal of water, on the other hand, brings about a retardation or negative variation in the rate of growth. Protoplasmic activity underlies both the movement of growth and the ascent of sap.

Effect of Gain or Loss of Water on Motile and Growing Organs

In my previous work, "The Motor Mechanism of Plants," it has been shown that the response of a motile organ is

TABLE IV.—EFFECT OF ALTERNATE VARIATIONS OF TURGOR ON GROWTH (ZEPHYRANTHES)

Condition of experiment	Rate of growth
Dry soil	0·04 μ per second
Application of warm water . .	0·20 μ ,, ,,
Steady growth after one hour .	0·08 μ ,, ,,
Application of KNO_3 solution . .	0·03 μ ,, ,,

essentially similar to that of a growing organ. Illustrative examples of this will be given in a later chapter. In order

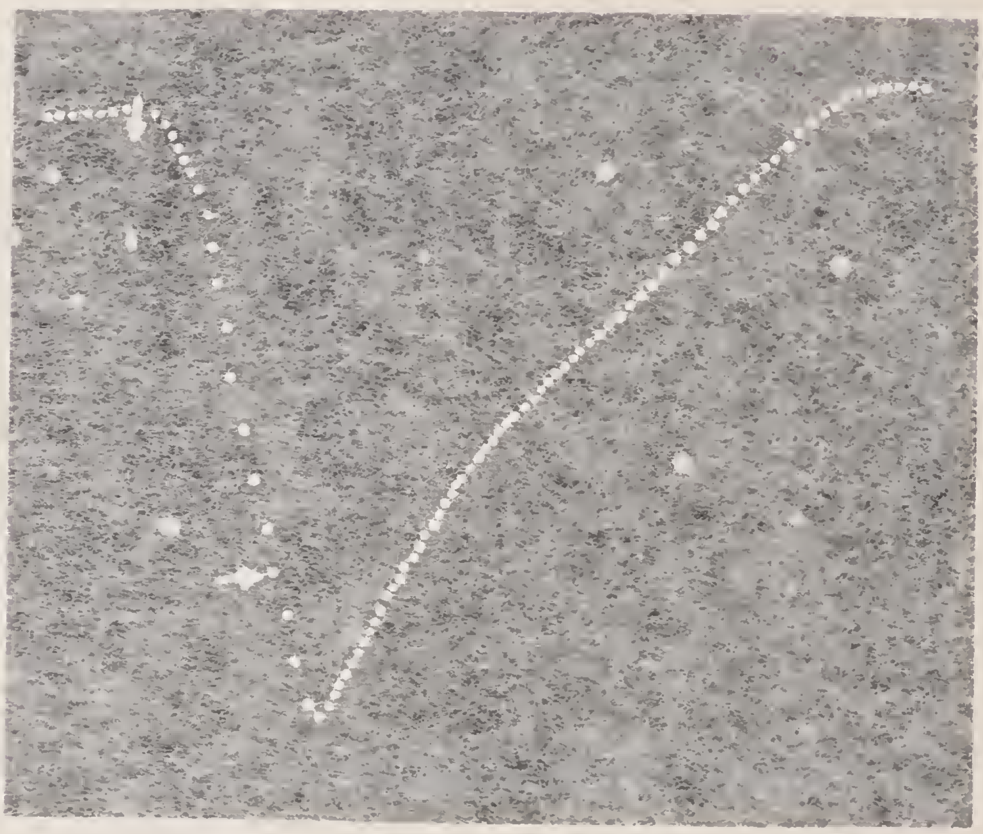


FIG. 10. Response of the pulvinus of Mimosa to irrigation and to withdrawal of water

Increased turgor by application of water at point marked with vertical arrow induced erectile movement. Diminution of turgor by application of KNO_3 solution at the point marked with the horizontal arrow brought about the fall of the leaf. Successive dots at intervals of 10 seconds. (The down-curve represents up-movement and *vice versa*.)

to observe the effect on a motile organ of the supply or withdrawal of water, Mimosa in a condition of drought may be taken, when its leaves are in a somewhat drooping

condition. The result of watering the roots is a renewal of suctional activity by which water is supplied to the pulvinus, causing its expansion and the erectile movement of the leaf. The record (fig. 26) exhibits this in a clear manner. Water was supplied to the root at the point marked by the vertical arrow, and the erectile movement occurred after 10 seconds, the delay being due to the time taken for the ascending water to reach the pulvinus. In order to ascertain the effect of withdrawal of water, a 5 per cent. KNO_3 solution was rapidly applied to the root at the horizontal arrow. The effect of the consequent withdrawal of water was the fall of the leaf, which occurred in the course of 40 seconds.

The increase of turgor by more rapid supply of water finds thus two parallel expressions, namely, an erectile movement of the leaf of Mimosa and an enhanced rate of growth in a growing organ. Withdrawal of water, resulting in a diminution of turgor, causes, conversely, a fall of the leaf and a retardation of the rate of growth.

Change of Turgor under Directive Movement of Sap

The movement of growth, as well as the erectile movement of a pulvinated organ, is generally ascribed to increase of turgor. But this cannot take place without an adequate supply of sap. The law which governs the directive movement of sap is that *it follows the stimulation gradient from the stimulated to the unstimulated region.*[1] The turgor is diminished at the point from which the sap is expelled, and becomes increased where the sap is accumulated.

The effects of quicker or slower rate of ascent of sap on movement of pulvinated and of growing organs are summarised under A and B.

[1] *The Motor Mechanism of Plants* (1928), p. 55.

A.

Enhanced rate of ascent of sap

Gain of water by the organ

Increase of Turgor

Erectile movement of Mimosa leaf. | Enhanced rate of growth in growing organ.

B.

Diminished rate of ascent of sap

Loss of water

Decrease of Turgor

Movement of fall of Mimosa leaf. | Retardation of rate of growth in growing organ.

The correspondence between the responsive movement of the leaf of Mimosa and that of variation in the rate of growth as explained above may be summarised as follows :—

1. An increase or positive variation of turgor due to enhanced rate of ascent of sap induces an erection or positive response of the leaf of Mimosa, and a positive variation or enhancement of the rate of growth.
2. A diminution or negative variation of turgor due to withdrawal of water induces a fall or negative response of the leaf, and a negative variation or retardation of the rate of growth.

Effect of Artificial Increase of Internal Hydrostatic Pressure

Experiment 31.—The plant was mounted watertight in the short limb of a **U**-tube, and subjected to increased hydrostatic pressure by increasing the height of water in the longer limb. The records were taken only when the rate of growth under the changed condition had become uniform, which occurs, generally speaking, in the course of about 5 minutes. Increasing internal hydrostatic pressure was found to increase the rate of growth up to a critical point, after which there was a decline. It is interesting to note that the motility of the pulvinus of Mimosa also undergoes a marked diminution under the condition of excessive turgor.

The critical pressure beyond which growth exhibits retardation is different in diverse species of plants. In Kysoor it is about 4 cm. pressure of water; in Crinum Lily it is as high as 30 cm. The curve which gives the relation between internal pressure and rate of growth is **S**-shaped. It rises slowly in the first part, and more quickly in the second; it then becomes horizontal and finally reversed, indicative of retardation.

The following tabular statement gives the effect of increased internal hydrostatic pressure on the rate of growth in two different specimens of Kysoor.

Table V.—Effect of Increased Hydrostatic Pressure on Growth.

Specimen	Hydrostatic pressure	Rate of growth
No. I.	Normal	0·18 μ per second
	2 cm. pressure	0·20 μ ,, ,,
	4 cm. ,,	0·11 μ ,, ,,
No. II.	Normal	0·13 μ ,, ,,
	1 cm. pressure	0·20 μ ,, ,,
	3 cm. ,,	0·18 μ ,, ,,
	4 cm. ,,	0·15 μ ,, ,,

Effect of External Tension

Excessive tension is usually found to retard the rate of growth. This is one of the defects of the ordinary auxanometer, in which the recording lever exerts a considerable pull on the plant.

Experiment 32.—The effect of gradual increase of tension on growth is observed as follows. The recording levers of the Crescograph are at first so balanced that very little tension is exerted on the plant, the record now giving the normal rate. The tension is then gradually increased from 1 grm. to 10 grm. When the growing organ is subjected to an increase of tension, the immediate effect is an excitatory contraction. But this transient effect disappears in a short time, after which it is easy to observe the permanent effect of tension on the rate of growth.

Table VI.—Effect of Tension on Growth (Crinum).

Tension	Rate of growth
0 (Normal)	0·4[illegible] μ per second
4 grams	0·44 μ ,, ,,
6 ,, ...	0·45 μ ,, ,,
8 ,, ...	0·52 μ ,, ,,
10 ,, ...	0·40 μ ,, ,,

The results given in the table above were obtained with Crinum; they show that the growth-rate increases with tension till a limit is reached, after which there is retardation.

Summary

Increase of turgor due to rise of sap after irrigation enhances the rate of growth. Enhanced rate of the ascent caused by irrigation with warm water induces a further augmentation of the rate of growth.

The length of the latent period preceding the enhancement of growth depends on the distance of the growing

region from the irrigated root. Irrigation with warm water reduces the latent period.

Diminution of turgor caused by withdrawal of water depresses the rate of growth.

Artificial increase of internal hydrostatic pressure up to a critical degree enhances the rate of growth.

The law of the directive movement of sap (which induces change of turgor) is that it follows the stimulation-gradient from the stimulated to the unstimulated region.

There is a correspondence between the responsive movement of the leaf of Mimosa and the movement of growth. An increase or positive variation of turgor, due to enhanced rate of ascent of water, induces the erection or positive response of the leaf of Mimosa, and the positive variation or enhancement of the rate of growth. A diminution or negative variation of turgor, due to withdrawal of water, induces the fall or negative response of the leaf of Mimosa, and the negative variation or retardation of the rate of growth.

External tension, within limits, enhances the rate of growth.

CHAPTER VII

EFFECT OF ELECTRIC STIMULATION ON GROWTH

In plant-physiology the word 'stimulus' is often used in a very indefinite manner. This is probably due to the different meanings which have been attached to the term. An agent is said to *stimulate* growth when it induces an acceleration of growth. The normal effect of stimulus is, as will be presently shown, the retardation of growth. It is probably on account of lack of precision in the use of the term that statements are often vaguely made of a stimulus sometimes accelerating and at other times retarding growth. In order to avoid any ambiguity, the terms *stimulus* and *stimulation* are here used in a sense as definite as in animal physiology. An induction electric shock, a sudden variation of temperature, mechanical stimulation, for example, bring about excitatory contraction in the muscle. These various forms of stimulation also cause excitatory contraction of the motile pulvinus of *Mimosa pudica*. The question suggests itself whether such diverse forms of stimulation evoke similar or different reactions in the growing organ.

An opinion prevails, however, that different modes of stimulation induce reactions which are specifically different. The results of investigation to be given in this and in the following chapters will show that this is by no means the case; for all kinds of stimulation of effective intensity induce excitatory response of the nature of mechanical contraction and of electromotive variation of galvanometric negativity. The perception of the stimulus and the consequent reaction ultimately arise from the excitation

of sensitive protoplasm. This is sometimes facilitated by special anatomical structures such as tactile hairs, by which mechanical stimulus becomes accentuated, and by lens-shaped epidermal cells for focusing the stimulus of light on the protoplasm.

In regard to the effect of different modes of stimulation on growth, the subjects to be considered in this and subsequent chapters are the following:

1. The Effect of Electric Stimulation.
2. The Effect of Stimulus of Light.
3. The Effect of Mechanical Stimulation.
4. The Effect of Thermal Radiation.
5. The Effect of Stimulus of Gravity.

Effect of Electric Stimulation

A form of stimulation which is extensively used in physiological investigations is the electric stimulus of an induction

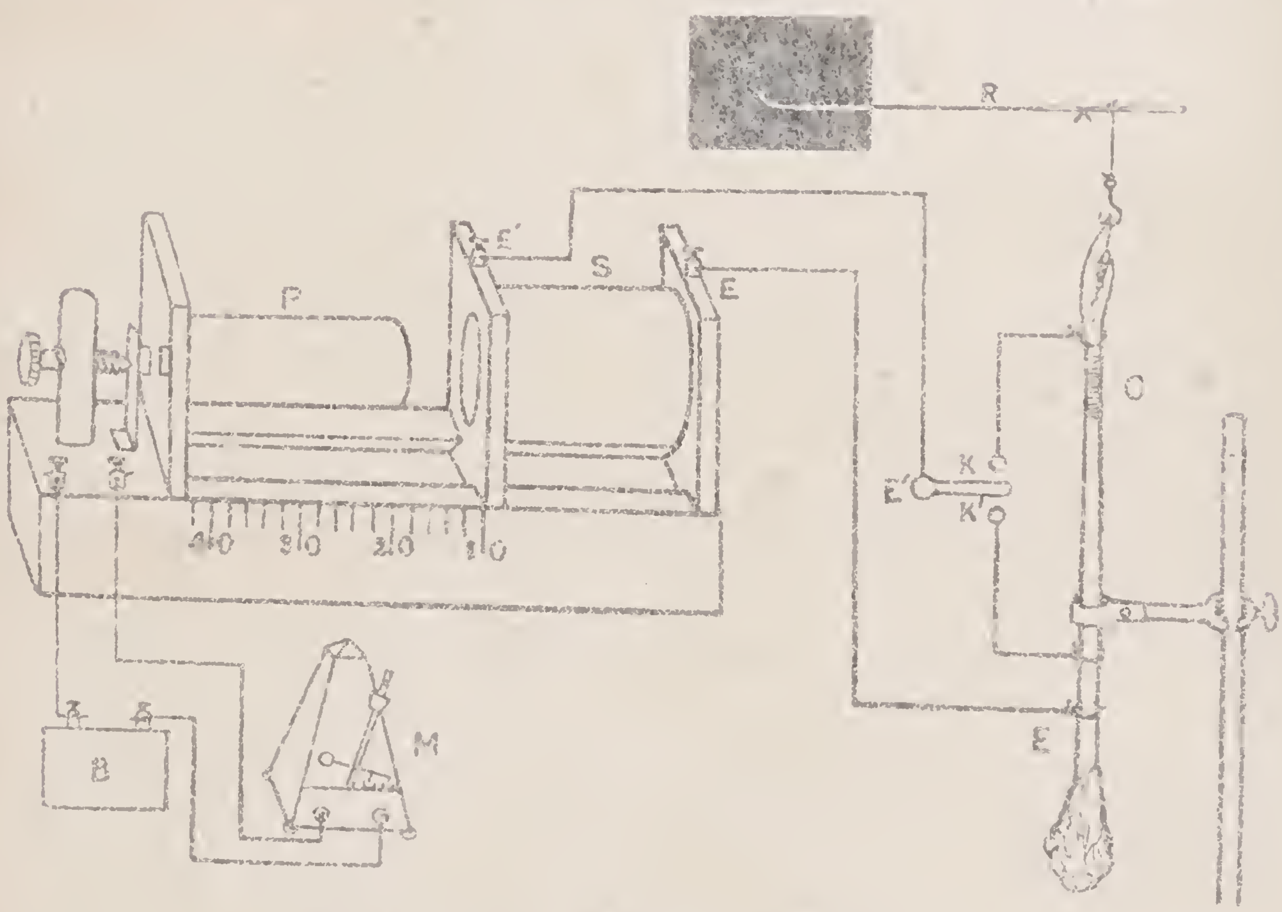


Fig. 27. Induction Coil. (See text.)

shock, which can be easily graduated by the use of the well-known sliding induction coil (fig. 27), in which the

approach of the secondary to the primary coil, indicated by the higher reading of the scale, gives rise to increasing intensity of stimulation.

Determination of Latent Period and Time-Relations of Response

Experiment 33. *Latent period in electric stimulation.*—A feeble current was applied for 1 second to the growing region of a bud of Crinum Lily by means of two electrodes, one above and the other below. The record was taken on a moving plate, the magnification employed being 2000 times, and the successive dots made at intervals of 2 seconds. It was a matter of surprise that the growth of the plant was affected by an intensity of stimulus below even the limit of human perception. As regards the relative sensitiveness of the plant and the animal, experiments described elsewhere show that the leaf of *Mimosa pudica*, when in favourable condition, responds to an electric stimulus which is one-tenth the minimum intensity that causes perception in a human being. For convenience, I designate the intensity of induction current that is barely perceptible to man as the unit of electric stimulus.

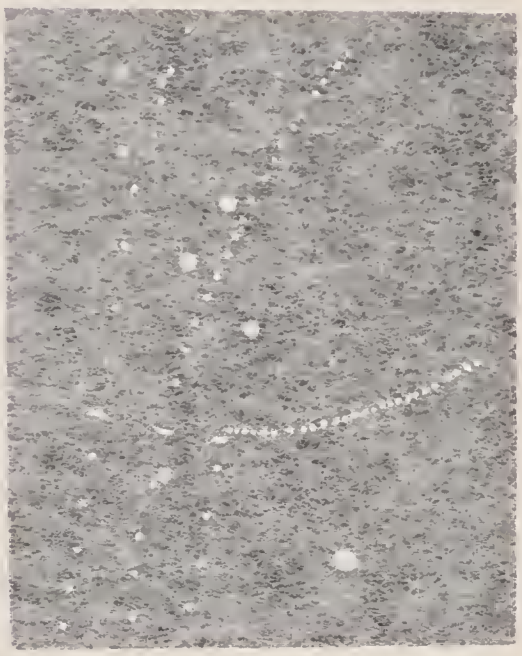


FIG. 28. Time-relations of the response of a growing organ to electric stimulus of increasing intensity.

Moment of stimulation shown by thick horizontal line. Successive dots at intervals of 2 seconds. (Crinum).

When an intensity of 0·25 unit was applied to the growing organ, it responded to it by a retardation of growth. Inspection of fig. 28 shows that a flexure was induced in the curve in response to the stimulus denoting retardation of growth. The latent period in this case was 8 seconds.

The normal rate was restored after 5 minutes. The intensity of current was next raised from 0·25 unit to 1 unit. The second record shows that the latent period was reduced to 4 seconds, and a relatively greater retardation of growth occurred under the action of the stronger stimulus. The recovery to the normal rate was not attained until after a period of 10 minutes. The intensity of stimulus was finally raised to 3 units; the latent period was now reduced to 1 second; the retardation induced was so great as to cause a temporary arrest of growth.

TABLE VII.—TIME-RELATIONS OF RESPONSIVE GROWTH VARIATION UNDER ELECTRIC STIMULATION (CRINUM).

Intensity of stimulus	Latent period	Normal rate	Retarded rate
0·25 unit	8 seconds	0·62 μ per second	0·40 μ per second
1·0 ,,	4 ,,	0·62 μ ,, ,,	0·25 μ ,, ,,
3·0 units	1 second	0·62 μ ,, ,,	Temporary arrest of growth

EFFECT OF INTENSITY AND DURATION OF STIMULATION

In the last experiment the effect of increasing intensity of stimulation in shortening the latent period and in prolonging the period of recovery was observed. In the two following experiments the effect of increasing intensity and duration of stimulus was the special object of investigation. The specimens employed were the buds of Crinum Lily, which were subjected to successive increase of intensity of stimulation. After each record sufficient time was allowed for recovery before application of the next stimulation.

Experiment 34. *Effect of increasing intensity of stimulation.*—The duration of the stimulation, which was 5 seconds, was kept the same in successive records, the intensity being increased from 1 to 2, and finally to 4 units. The normal

rate of growth of the bud of Crinum Lily was 0·35 μ per second. On the application of electric stimulus of unit intensity for 5 seconds, the rate became reduced to 0·22 μ per second. When the stimulus was increased to 2 units, the rate of the retarded growth was 0·07 μ per second. When the intensity was raised to 4 units, there was complete

Fig. 28. Records of contractile response under increasing intensities of electric stimulation of 0·25, 1, and 3 units

Records to be read from above downwards. Short vertical lines indicate moments of application of stimulus (Crinum).

arrest of growth. In fig. 29 are given records of another series of experiments which show the effects of increasing intensity of stimulation in retarding growth.

Experiment 35. *Effect of continuous stimulation.*—The effect of continuous electric stimulation of increasing intensity will be seen in the record (fig. 30) taken on a moving plate. On application of continuous stimulation of increasing intensity, an increased flexure was produced in the curve, which denoted greater retardation in the rate of growth.

When the intensity of stimulus was raised to 3 units there was an actual contraction.

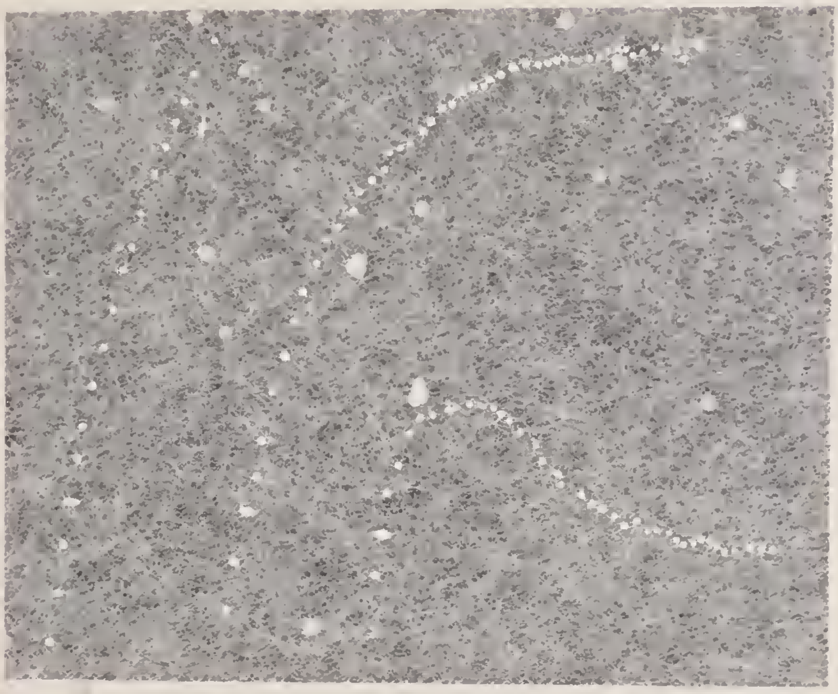


FIG. 30. Effect of continuous electric stimulation. Intensities of stimuli, 0·5, 1, and 3 units; corresponding records from left to right.

Note actual shortening of the organ under 3 units (Crinum).

CONTINUITY BETWEEN INCIPIENT AND ACTUAL CONTRACTION

It will thus be seen that external stimulation induces a reaction which is of opposite sign to that of normal growth-elongation. This retardation may be conveniently described as 'incipient' contraction; for under increasing intensity of stimulus the contractile reaction opposing growth-elongation becomes more and more pronounced; at an intermediate stage this results in an arrest of growth; at a further stage it culminates in an actual shortening of the organ. There is no break of continuity between these stages. I shall, therefore, use the term 'contraction' in a wider sense, including the 'incipient' stage which finds expression in retardation of growth.

In Table VIII are given the results of typical experiments on the effect of stimulation of increasing intensity and duration.

TABLE VIII.—EFFECT OF INTENSITY AND DURATION OF ELECTRIC STIMULATION ON GROWTH (CRINUM).

Duration of application	Intensity	Rate of growth
5 seconds	Normal	0·35 μ per second
,,	1 unit	0·22 μ ,, ,,
,,	2 units	0·07 μ ,, ,,
,,	4 ,,	Arrest of growth
Continuous stimulation	Normal	0·30 μ per second
,, ,,	0·5 unit	0·20 μ ,, ,,
,, ,,	1 ,,	0·09 μ ,, ,,
,, ,,	3 units	Contraction

CONTRACTILE RESPONSE OF PULVINATED AND OF GROWING ORGANS

Very striking is the similarity between the contractile response of the leaf of Mimosa and that of the growing organ. For the purpose of comparison I first give the record of Mimosa under moderate electric stimulation. The up-curve exhibits the contractile movement, the successive dots being at intervals of a tenth of a second; the recovery is slow, and the successive dots in the down-curve are at intervals of 10 seconds (fig. 31).

FIG. 31. Contractile response of leaf of Mimosa.

Up-curve (successive dots at intervals of 0·1 second) indicates responsive contraction. Down-curve shows recovery (successive dots at intervals of 10 seconds).

Experiment 36. *Contractile response of a growing organ.*—A very similar response was obtained with a growing bud of Crinum under electric stimulation of moderate intensity, the recorder employed giving a magnification of 1000 times. In fig. 32 the normal

growth-elongation is represented as a down-curve. On the application of stimulus, the normal expansion was suddenly reversed to excitatory contraction; the latent period was 1 second, and the period of attainment of maximum contraction 4 minutes. The organ recovered its original length after a period of 7 minutes. Repeated stimulation gave rise to repeated responses as in the case of Mimosa.

FIG. 32. Contractile response of a growing organ under electric shock (Crinum).

Successive dots at intervals of 4 seconds. Vertical lines below represent intervals of 1 minute. (Magnification 1000 times.)

Arbitrary Distinction between Responses of Pulvinated and Growing Organs

The growing organ, when subjected to successive stimulations, *gives a contractile response in every way similar to the mechanical response of Mimosa*. An arbitrary distinction has been drawn between the response of pulvinated and that of growing organs. The movement of the former has been distinguished as one of variation adapted for repetition an infinite number of times, whereas a growing organ has been supposed to be incapable of exhibiting repeated response. The experiment described proves that there is no such basic distinction between the two classes of phenomena.

Summary

In normal conditions, electric stimulation induces incipient contraction exhibited by retardation of the rate of growth. Growth may be affected by an intensity of stimulation below the range of human perception.

The latent period in the responsive variation of growth is shortened under stronger stimulus, but the period of recovery becomes protracted.

Under increasing intensity of stimulation the contractile reaction becomes more and more pronounced. At a critical intensity of stimulus, growth becomes arrested; under a still stronger intensity there is an actual shortening of the organ. Continuity thus exists between incipient and actual contraction.

The distinction between the responses of pulvinated and growing organs is arbitrary. Growing organs are capable of repeated response, just as are pulvinated organs.

CHAPTER VIII

EFFECT OF LIGHT ON GROWTH

I SHALL first deal with the effect of light on vigorously growing organs, leaving the consideration of the abnormal reaction to light, the underlying cause of which was at first difficult to trace, for the next chapter. The effect of light is studied by taking the normal record of growth in darkness or under uniformly diffused feeble light, and then records under increasing intensities of illumination. The subjects discussed in the present chapter are:

1. Normal effect of light on growth.
2. Determination of the latent period of response.
3. Effect of increasing intensity of light.
4. Effect of continuous stimulation.
5. Immediate and after-effect of light.
6. Effects of different rays of the spectrum.

METHOD OF EXPERIMENT

The plant was placed in a glass chamber kept moist. Strong light was obtained from a small arc-lamp with a self-regulating device for ensuring steadiness of illumination. An incandescent electric bulb was also employed as a less strong source of light. Two inclined mirrors were placed close behind the plant so that light acted on it from all sides.

NORMAL EFFECT OF LIGHT

Experiment 37.—The record of normal growth N, of Kysoor, was at first taken in darkness on a stationary plate.

[illegible]

of growth (fig. 33). For the same extent of growth-elongation there are 12 spacings in darkness and 24 spacings in

FIG. 33. Effect of light in retardation of growth.
N, normal; S, retarded rate in response to light; N′, recovery half an hour after cessation of light (Kysoor).

light. The rate of growth under the action of light was thus reduced to half. Record N′ was taken once more in darkness after an interval of half an hour, showing restoration of the normal rate.

THE LATENT PERIOD

A prevalent impression exists that a considerable period, from several minutes to an hour, intervenes between the incidence of light and the responsive variation of growth. This over-estimate must be due to the absence of sufficiently

delicate means of observation; for my High Magnification Recorder indicated, in some cases, response within a period as short as 5 seconds of exposure to light. In other cases the latent period was found to vary from 15 seconds to several minutes.

Experiment 38. *Determination of the latent period.*—The record of the effect of an arc-light on a seedling of

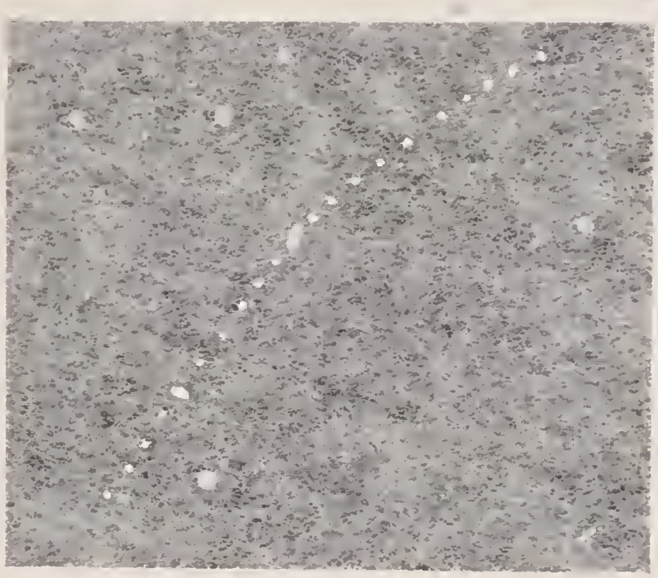


FIG. 34. Determination of the latent period.
Light applied at thick dot. Successive dots at intervals of 5 seconds (Cucurbita).

Cucurbita was taken on a moving plate (fig. 34). The first part of the record gives the normal rate of growth; light was applied at the thick dot, and the flexure of the curve after the seventh dot indicates the responsive retardation. As the successive dots are at intervals of 5 seconds, the latent period in this case was 35 seconds.

Effect of Increasing Intensity of Light

Experiment 39.—The specimen employed was Crinum; it was subjected to light emitted by a half-watt incandescent electric lamp of 200 candle-power. The intensity of light when the lamp was placed at a distance of 100 cm. from the plant was taken as the unit. Much feebler light would

have been sufficient, but would have required a very long exposure. The intensity was increased by bringing the lamp nearer the plant; marks were made on a horizontal scale so that the intensity of incident light increased at the successive marks of the scale as 1 : 2 : 3, and so on. The duration of exposure was the same in all cases, namely, 5 minutes. After each exposure to light, suitable periods of rest were allowed for the plant to recover its normal rate of growth. The records in fig. 35 show increasing retardation induced by stronger intensities of light. Table IX gives the result obtained with another specimen.

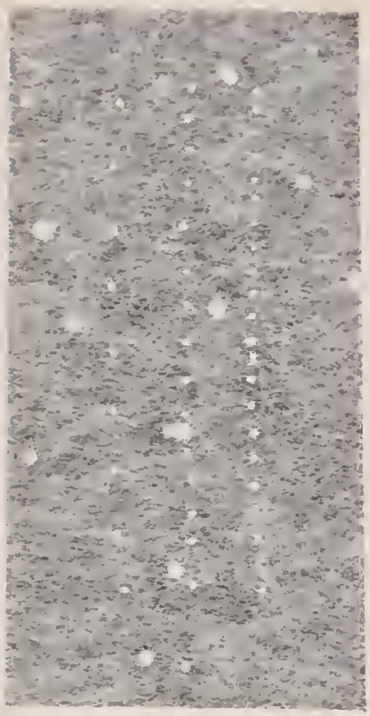


FIG. 35. Effect of light of increasing intensity in retardation of growth.
First record normal; second and third records under intensities of 2 and 3 units (Crinum).

EFFECT OF CONTINUOUS LIGHT

Experiment 40.—The effect of continued light of moderate intensity in bringing about increasing retardation of growth will be seen in fig. 36, *b*, side by side with the record of effect of continuous electric stimulation of constant intensity on growth (fig. 36, *a*). In both cases the effect of continuous stimulation is seen to be essentially similar, namely, increasing retardation culminating in arrest of growth. This is true

TABLE IX.—EFFECT OF LIGHT OF INCREASING INTENSITY ON THE RATE OF GROWTH (CRINUM).

Intensity of light	Rate of growth
0 (Normal)	0·47 μ per second
1 unit	0·29 μ ,, ,,
2 units	0·17 μ ,, ,,
3 ,,	0·09 μ ,, ,,
4 ,,	Arrest of growth

of stimulus of moderate intensity. Under a more intense stimulation the incipient contraction does not end in the arrest of growth, but the responding organ undergoes an actual shortening of its length.

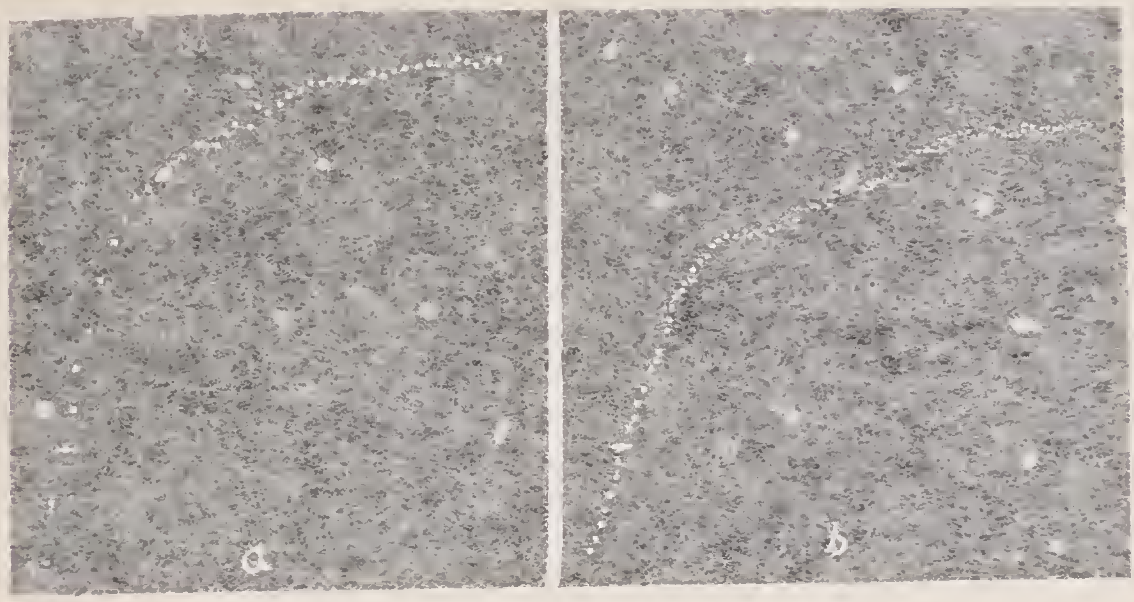


Fig. 36. Effects of continuous (*a*) electric and (*b*) photic stimulation recorded on a moving plate (Crinum).

Immediate and After-Effect of Light

The Balance Method of observation offers, as previously indicated, a unique opportunity of discovering the characteristics of different responsive phases, both during the exposure and after the cessation of light. I will describe two illustrative examples with two different species of plants, one of which was in a vigorous condition of growth, while the other was in a slightly subtonic condition.

Experiment 41. *Direct and after-effect of light.*—The specimen was a flower-stalk of Allium mounted on the Balanced Crescograph. The index showed the normal rate of growth to be 0·37 μ per second. After obtaining the balance, the plant was subjected to light from a small arc-lamp, being illuminated on all sides by suitably inclined mirrors. The successive dots in the record are at intervals of 10 seconds. The moment of incidence of light is indicated by a vertical arrow, and cessation of light by a horizontal arrow within a circle (see fig. 37).

The record shows that the balance, after a latent period of 40 seconds, was upset upwards, indicative of retardation of growth. The total duration of application of light was about 5 minutes; the retardation persisted for a further period of a minute and a half. After this the rate of growth became normal for about 2 minutes, as seen in the approximately horizontal record at the top of the curve

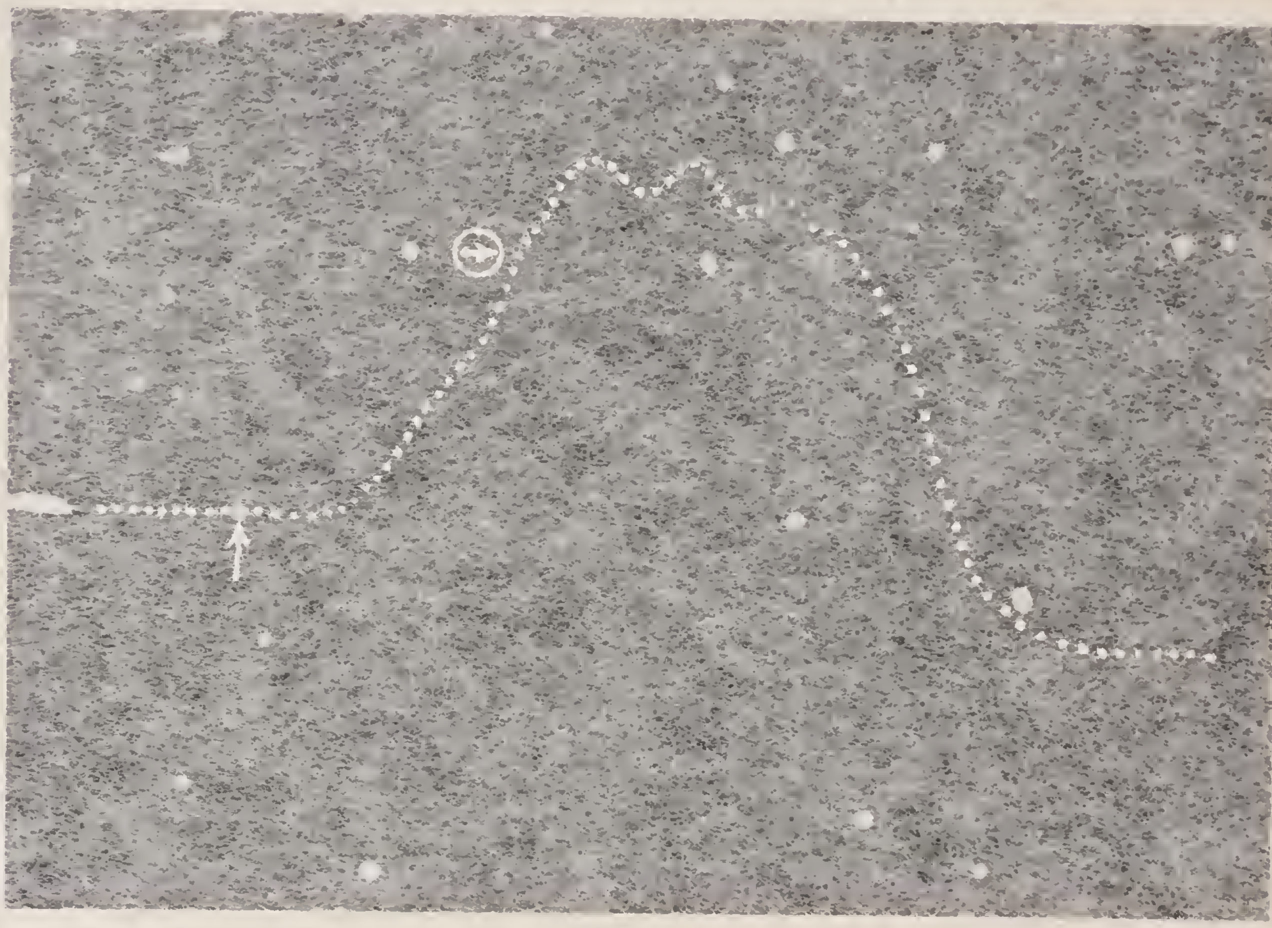


FIG. 37. Direct and after-effect of light recorded by Method of Balance (Allium).

characterised by two small pulsations. The most interesting after-effect of stimulation by light was then exhibited in the down-curve, indicative of enhancement of the rate of growth above the normal, which persisted for 8 minutes. After this, the growth-rate was restored to normal as indicated by the horizontal record (fig. 37).

Experiment 42. *Effect on a slightly subtonic specimen.*—A seedling of Wheat was mounted on the Balanced Crescograph and record was first taken under exact balance, giving a horizontal line. Light from the arc-lamp was now applied for a few minutes. The record shows, by the

preliminary down-curve, a transitory acceleration of growth. This was followed by the normal retardation as shown by the up-curve. On the cessation of light, there was a restoration of the normal rate as seen in the horizontal record at the top of the curve; but after a while the balance was upset in the opposite direction, exhibiting a rate above the normal. Finally, the rate of growth became restored

FIG. 38. Response of subtonic specimen to stimulus of light. Note preliminary acceleration of growth followed by retardation (up curve); after-effect, an enhanced rate of growth followed by recovery (seedling of Wheat).

to the normal, as seen in the curve becoming once more horizontal (fig. 38).

The curves given in figs. 37 and 38 are essentially similar. The only difference is in the preliminary acceleration of growth which, as will be shown in the next chapter, is the temporary effect of stimulation on a subtonic tissue.

A second record was taken with the identical specimen, the intensity of light being increased by bringing the arc-light nearer the plant. In this experiment retardation of growth occurred from the very beginning. This was for two reasons: (1) the increased intensity of light was now

above the critical minimum which will be shown later to demarcate the abnormal from the normal response; (2) the tonic condition of the organ was now improved by previous stimulation.

The important result regarding the after-effect of moderate intensity of light is that, for a brief period, the rate of growth is enhanced above the normal. This will be shown to be the characteristic after-effect of all modes of stimulation, being a factor of much importance in accelerating the recovery of the organ from the effect of brief stimulation.

Effects of Different Rays of the Spectrum

Previous observers have found that it is the more refrangible rays which exercise the greatest influence upon growth and tropic curvature. The relative effects of lights of different colours are, however, more precisely indicated by the curve of response to the action of different rays. For this purpose I first employed monochromatic light from different parts of the spectrum, produced by a prism of high dispersion. In practice the usual colour-filters were found very convenient, as they allow the application of more intense light. Certain complications arise from the slight rise of temperature due to the absorption of radiant energy by the organ. Moderate rise of temperature has been shown to enhance the rate of growth (p. 36), while radiation, in general, causes a retardation. In spite of this, it is easy to demonstrate the predominant effect of certain rays in retarding growth.

Experiment 43. *Effect of red and of yellow light.*—The highly sensitive Balanced Method of record fully supported the results previously obtained, that these rays are practically ineffective in inducing any retardation in the rate of growth.

Experiment 44. *Effect of blue light.*—On application of light even for such a short period as 34 seconds, the effectiveness of the blue rays became fully demonstrated. For the

responsive retardation occurred in the course of 14 seconds and the depression of the rate was two-fifths of the normal.

Experiment 45. *Effect of infra-red rays.*—In passing from the highly refrangible blue to the less refrangible red rays, the responsive retardation of growth undergoes a diminution or even abolition. Proceeding further into the infra-red region of thermal rays, these are found to become highly effective in inducing very marked retardation in the rate of growth.

The curve drawn with the wave-length of light as abscissa, and the effectiveness of the ray as ordinate, shows a fall towards zero from the blue to the red; the curve however shoots up on proceeding further into the region of the infra-red towards the invisible thermal rays.

SUMMARY

The normal effect of light is retardation of the rate of growth, which is, in fact, incipient contraction.

The latent period may in some cases be as short as 5 seconds, in others it varies from 15 seconds to several minutes. The latent period is shortened under stronger intensity of light. Increasing intensity of light induces increasing retardation culminating in an arrest of growth.

The response to continuous stimulation by light is essentially similar to that to continuous electric stimulation.

The after-effect of brief and moderate stimulation by light is a short-lived acceleration of growth above the normal rate.

The effectiveness of different rays of the visible spectrum in retarding growth undergoes a decline from the blue to the red rays. The thermal rays in the infra-red region are, however, very effective in retarding growth.

CHAPTER IX

ACCELERATION OF GROWTH IN SUBTONIC PLANTS ON STIMULATION

After investigation of the normal effect of electric and photic stimulation in retarding growth, described in the two previous chapters, it was a matter of considerable surprise to me that the responses were occasionally *positive*; that is to say, an acceleration of growth instead of the normal *negative* response of retardation. After giving an account of these positive responses, I shall attempt to trace the cause of the abnormality.

Acceleration of Growth under Light

Experiment 46.—The specimen employed was Kysoor, which was exposed to the action of strong light for 5 minutes. Its normal rate of growth was $0 \cdot 3\ \mu$ per second; but after exposure to light there was an enhancement of the rate of growth to $0 \cdot 40\ \mu$ per second.

The plant was then subjected to the continued action of light for half an hour, which caused a transformation of the response from the abnormal positive acceleration to the normal negative retardation of growth. The question now arises: What is the characteristic of the organ which predisposed it to give a positive response, and how did the positive response at the beginning become transformed into the normal negative under the continued action of light?

Referring to fig. 33 (p. 72), in which normal retardation of growth occurred in Kysoor, it was found that its rate of growth was as high as $0 \cdot 8\ \mu$ per second. But in Experiment 46, in which there was an acceleration of growth

under stimulation, the rate of growth of that particular specimen of Kysoor was feeble, being as low as 0·3 μ per second. As the activity of growth is an indication of a healthy tone, the enfeebled rate of growth was a sign of the subtonic condition of the plant. It thus appeared that, other things being the same, the abnormal positive is the characteristic response of the subtonic plant.

In the parallel phenomenon of response of a pulvinated organ such as the leaf of Mimosa, I have shown (1) that when the tonic level of the pulvinus is *below par*, the response is abnormal positive, exhibited by the erectile movement of the leaf, and (2) that as a result of continuous stimulation the tonicity is raised to a condition of *par*. The response is now changed into normal negative as indicated by the fall of the leaf.[1] In the responsive variation of growth, likewise, the abnormal positive response of the subtonic specimen was transformed into the normal negative in consequence of improvement of tonic condition attained under continued photic stimulation. The above facts lead to the following generalisation:

1. That while strong light induces *retardation* of growth in an organ whose tonic condition is normal or *above par*, it induces *acceleration* in an organ whose condition is *below par*;
2. That by the action of the stimulus of light itself, a subtonic organ is raised to a condition of *par*, with concomitant transformation of its response to that of normal retardation.

Continuity between Abnormal and Normal Response

The tonic condition of a growing organ may vary widely; of this the following are the two extreme cases: (1) the optimum, and (2) the subtonic. In the optimum condition

[1] *The Motor Mechanism of Plants* (1928), p. 51.

the rate of growth is very rapid, while in the subtonic growth is feeble or even arrested. There are all possible gradations between the two extremes.

The responsive reaction depends then on two important factors: the tonic condition of the organ and the effective intensity of stimulation. The effectiveness of stimulation is determined, not only by its intensity, but also by its duration.

These theoretical conclusions may be summarised thus:

1. A subminimal stimulus is gradually transformed into a minimal and then to a maximal, under prolonged duration of stimulation.

2. A strong stimulus may prove to be subminimal for a short time at the moment of its application, specially when the organ is in a slightly subtonic condition.

The possible combinations of the effects of these varying factors are very numerous, and it is therefore necessary to confine attention to the typical cases which, from the theoretical point of view, may be expected to give the positive response of enhanced rate of growth:

First, a normal organ under short exposure to a subminimal stimulus; and

Secondly, a subtonic organ under moderate and not excessively prolonged stimulation.

Enhanced Rate of Growth under Subminimal Stimulation

Experiment 47.—The abnormal positive response was obtained even with a moderately vigorous specimen, when the intensity of the incident light was feeble, as seen in the record of growth taken on a moving plate (fig. 39). The slope of the first part of the curve shows the normal rate; stimulus was applied for a short time at the fifth dot, and the sudden erection of the curve demonstrates the enhanced rate of growth. This persisted for a time, after which the rate returned to the normal. Continued exposure

to feeble light, or to stronger light, converted the acceleration into the normal retardation.

Opposite effects of feeble and strong stimulation.—Thus while strong stimulation induces retardation of the rate of growth, feeble stimulation causes an enchancement of the rate. In the wide range of stimulation between minimal and maximal there is therefore a critical intensity above which there is a retardation and below which there is

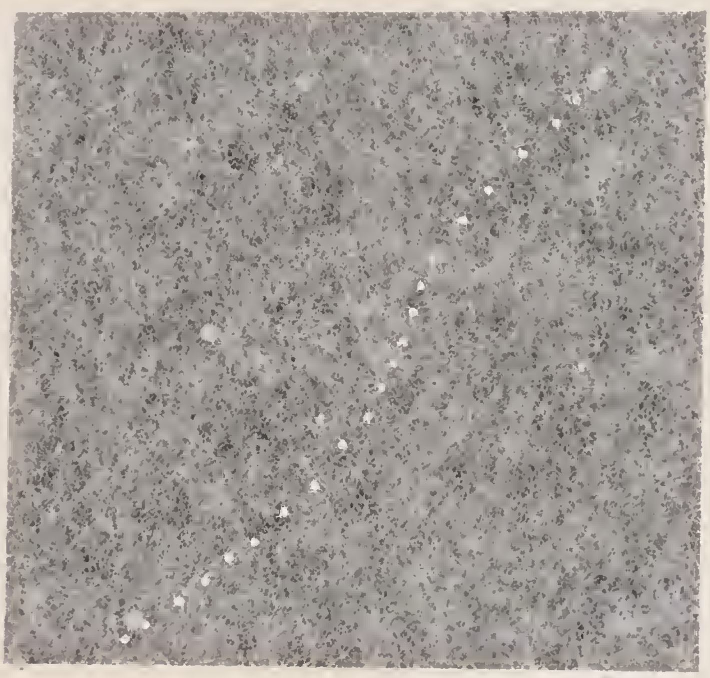


FIG. 39. Acceleration of growth under subminimal stimulus of light (Kysoor).

an acceleration. This critical intensity varies in different species of plants.

As chemical substances often cause stimulation, the opposite effects of small or large doses of the same drug may perhaps afford parallel phenomena.

REVIVAL OF GROWTH PREVIOUSLY AT STANDSTILL

Experiment 48.—An organ falls to a condition of extreme subtonicity when it is maintained for a long time under unfavourable conditions. A peduncle of Allium was kept in the dark for a fortnight, after which its growth was found to have been practically arrested. The plant attached to the Crescograph then gave an almost horizontal record on

a moving plate. Exposure to strong light from an arc-lamp for 4 minutes was, however, effective in reviving the growth, as indicated by the erection of the curve (fig. 40). In a vigorous specimen of Allium, on the other hand, the effect of light has been shown to be a retardation of growth (*cf.* fig. 37). *The results offer conclusive evidence that the sign of response, negative or positive, is dependent on the tonic condition of the organ.*

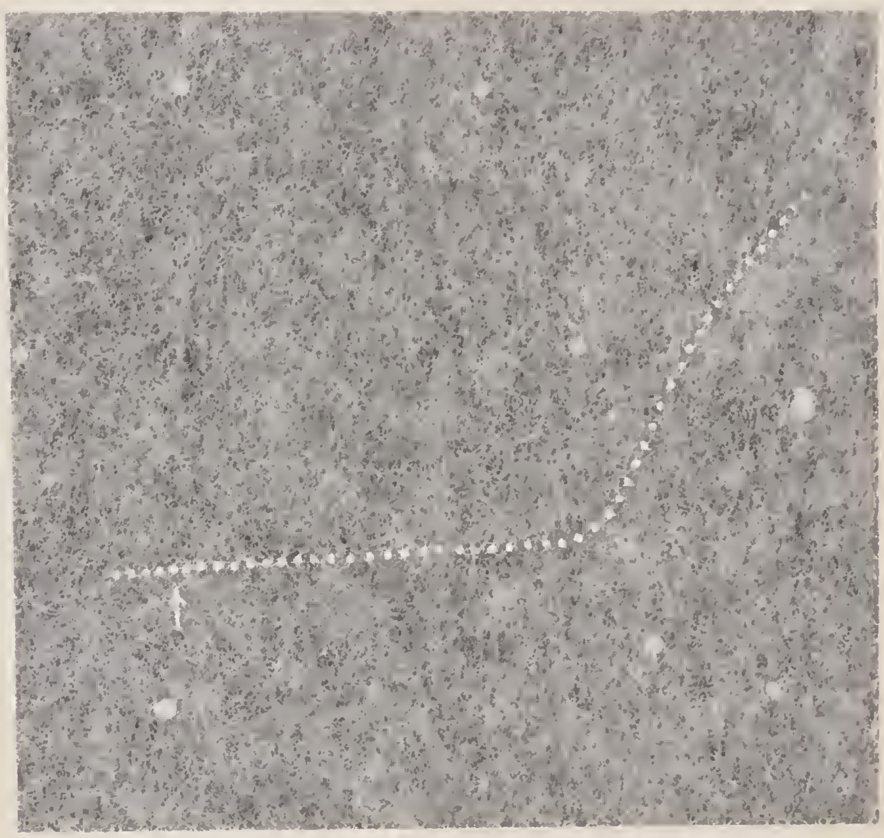


FIG. 40. Stimulus reviving growth at standstill (Allium).

The next problem to be considered is whether the acceleration of growth in a subtonic organ under light is due to its action as a stimulus, or to its possible photosynthetic effect. The experimental specimens usually employed were flower-stalks or stems in which chlorophyll was absent. The question can, however, be finally settled by finding whether a different form of stimulus, such as a tetanising electric current, which cannot possibly exert any photosynthetic action, also induces acceleration of growth in a subtonic organ.

Acceleration of Growth under Electric Stimulation

Experiment 49.—I took a subtonic seedling of Wheat, whose rate of growth was as low as 0·05 μ per second. After electric stimulation, the rate was found to be enhanced to 0·12 μ per second or about $2\frac{1}{2}$ times. I give two records obtained with different specimens (fig. 41). The two vertical records to the left of the figure were taken

Fig. 41. Electric stimulation enhancing rate of growth of subtonic plant (Wheat).

N, normal record; S, after stimulation.

on a stationary plate. The closeness of the dots in N shows the feeble rate of growth of the subtonic specimen. After application of electric stimulus the record S shows, by the wider spacings between successive dots, the induced enhancement of growth.

In the second experiment the records (fig. 41, b) were taken on a moving plate. The specimen was so extremely subtonic that its normal record N appears almost horizontal. The marked erection of the curve S after stimulation demonstrates the induced acceleration of growth.

TABLE X.—ACCELERATION OF GROWTH IN SUBTONIC SPECIMENS BY ELECTRIC AND PHOTIC STIMULATION.

Specimen	Stimulus	Rate of growth
Wheat seedling	Normal After electric stimulation	0·05 μ per second 0·12 μ ,, ,,
Kysoor . .	Normal After 5′ exposure to light	0·30 μ per second 0·40 μ ,, ,,

The effect of direct stimulation upon growth has thus been shown to be modified by the tonic condition of the plant, there being an enhancement of the rate when the plant is in a state of subtonicity. Is there any other condition under which stimulus enhances the rate of growth? I take up the question in a future chapter.

SUMMARY

The sign of the response of an organ is dependent on its tonic condition.

When the pulvinus of Mimosa is in a subtonic condition, the response to stimulation is positive, that is expansion and erectile movement, instead of the negative response of contraction and resulting fall of the leaf.

As the result of continuous stimulation the tonicity is raised to a condition of par, the abnormal positive response being converted into the normal negative.

The effect of stimulation on growth is modified in a parallel manner, according to the tonic condition of the organ.

When the organ is in a subtonic condition, it responds to stimulation by an enhancement of its rate of growth.

In extreme cases, growth in a state of standstill becomes revived under stimulation.

Continuous stimulation of a subtonic organ by light or by electric current raises the tonic condition of the growing tissue, the response of acceleration becoming transformed into one of normal retardation.

CHAPTER X

EFFECT OF MECHANICAL STIMULATION ON GROWTH

Amongst the mechanical stimuli which induce excitatory contraction in Mimosa may be mentioned the irritation caused by rough contact, by a prick or by a wound. Friction causes moderate stimulation, from which the excited pulvinus recovers within a short time. But a prick or a cut induces a far more intense and persistent excitation; the recovery becomes protracted, and the overstimulated pulvinus remains contracted for a long period.

I now describe the effect of mechanical irritation on growing organs, which will be found to be essentially similar to that on the pulvinus. For moderate stimulation I employ rough contact or friction; for more intense stimulation, a prick or a cut.

Effect of Mechanical Stimulation

Experiment 50.—The experiment was carried out with the peduncle of *Zephyranthes*, which had a normal rate of growth of 0·18 μ per second. It was subjected to mechanical stimulation, the surface being rubbed with a piece of cardboard. This caused a retardation of growth, the depressed rate being 0·11 μ per second, or three-fifths the normal rate. The normal rate of growth was restored after this moderate stimulation within a comparatively short period of rest. After 15 minutes the rate became 0·14 μ per second, and complete recovery was attained after an hour when the rate became 0·18 μ per second, as

at the beginning (fig. 42). The growth-rate is greatly depressed under intense stimulation, and the period of recovery then becomes very much protracted.

I have often been puzzled by the fact that specimens apparently vigorous exhibited little or no growth after attachment to the Crescograph. After waiting in vain for an hour, I had to discard them for others with equally

FIG. 42. FIG. 43.

FIG. 42. Effect of mechanical friction on growth.
N, normal rate; F, retarded rate immediately after friction; A, partial recovery after 15 minutes. Successive dots at intervals of 5 seconds (*Zephyranthes*).

FIG. 43. Effect of pin-prick on growth.
N, normal rate; W, immediate effect after wound; A, partial recovery after an hour (*Zephyranthes*).

unsatisfactory results. One of these specimens happened to be left attached to the recorder overnight, and I was greatly surprised to find that the specimen which had shown no growth the previous evening, now exhibited vigorous growth after being left to itself for 12 hours. I then realised that the temporary arrest of growth had been due to stimulation caused by the somewhat rough handling during the process of mounting and attachment of the specimen to the recorder.

The prolongation of the period of recovery after intense stimulation is demonstrated by the following experiments.

Effect of Wound

A prick causes an intense excitation in Mimosa; I tried the effect of this form of stimulation on a growing organ.

Experiment 51.—The specimen was the same as had been employed in the last experiment. After moderate stimulation by friction it had, in the course of an hour, completely recovered its normal rate of growth of 0·18 μ per second. The stimulus of a pin-prick was now applied; the actual injury to the tissue was relatively slight, but the retardation of growth induced by this relatively intense stimulation was very great. With moderate mechanical friction the rate had fallen from 0·18 μ to 0·11 μ per second, *i.e.* to three-fifths the normal rate; but the prick induced a depression of growth from 0·18 μ to 0·05 μ per second, *i.e.* to less than a third of the normal rate. After 15 minutes the rate recovered from 0·05 μ to 0·07 μ per second. After moderate friction the recovery was completed after an hour; but after the prick the recovery at the end of an hour was only three-fourths of the normal, the rate being now 0·12 μ per second (fig. 43). I next applied the more intense stimuation induced by a longitudinal cut. This caused a depression of the growth-rate to 0·04 μ per second. A transverse cut was found to be far more effective in retarding growth than a longitudinal slit.

Table XI.—Effect of Mechanical Stimulation and of Wound on Growth (Zephyranthes).

Nature of stimulus	Condition	Rate of growth
Mechanical friction	Normal rate	0·18 μ per second
	Immediately after stimulation	0·11 μ ,, ,,
	15 minutes after stimulation	0·14 μ ,, ,,
	60 ,, ,, ,,	0·18 μ ,, ,,
Prick with needle	Normal rate	0·18 μ per second
	Immediately after stimulation	0·05 μ ,, ,,
	15 minutes after stimulation	0·07 μ ,, ,,
	60 ,, ,, ,,	0·12 μ ,, ,,

The effect of mechanical stimulus on growth is thus similar to those of other modes of stimulation, such as electric and photic. Moderate frictional stimulation induces incipient contraction, shown by retardation of growth, recovery being completed within a short time; but intense stimulation, caused by a wound, gives rise to a greater and more persistent retardation.

I next describe the movement of curling induced in a tendril by unilateral mechanical stimulation.

MECHANOTROPISM: TWINING OF TENDRILS

In response to the stimulus of contact a tendril twines round its support. Certain tendrils are uniformly sensitive on all sides; but in other cases, as in the tendril of Passiflora, the sensitiveness is greater on the under side. A curvature is induced when that side is rubbed with a splinter of wood, the stimulated side becoming concave. This movement may be distinguished as one of *curling*. There are, as will be presently shown, instances where the under side becomes convex, the curvature being thereby reversed.

As regards contrivances for enhanced perception of mechanical stimulus by the tendril, Pfeffer discovered tactile pits on the tendrils of Cucurbitaceae. These no doubt facilitate sudden deformation of the sensitive protoplasm by frictional contact. No satisfactory explanation has, however, been offered as regards the physiological mechanism of the responsive movement.

The twining must result from the modification of the normal rate of growth under the stimulus of contact. Further, this modification must be different on the two sides of the organ: the proximal, on which the stimulus is directly applied; and the distal, on which the stimulus can only act indirectly. Investigations had therefore to be undertaken to detect and record the effect of direct stimulation, and also of indirect stimulation, that is, when the stimulus acts at a distance.

I have studied the effects of direct and indirect stimulation on the growth of the tendril, employing not only mechanical but also other kinds of stimuli as well, the fundamental reaction being essentially similar in all cases. I will first describe the effect of electric stimulation, since the impact of this stimulus does not produce any mechanical disturbance.

Effects of Indirect and Direct Electric Stimulation on the Growth of a Tendril

For this investigation I took a growing tendril of Cucurbita, the sensitiveness of which is more or less uniform

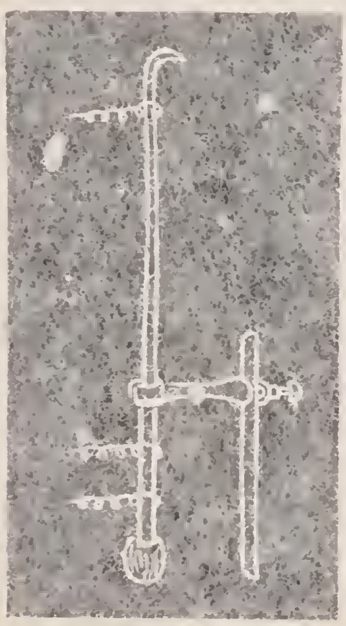


Fig. 44.

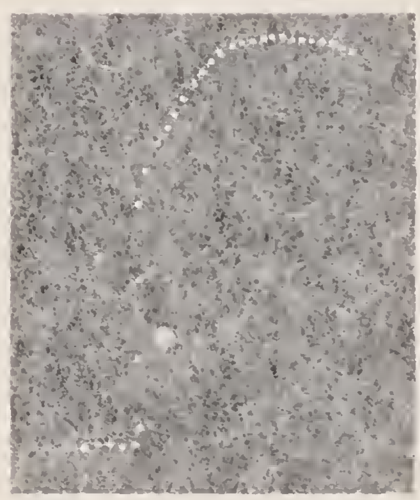


Fig. 45.

Fig. 44. Diagrammatic representation of Method for the Indirect and Direct Electric Stimulation of tendril.

Fig. 45. Record by Method of Balance, showing acceleration of growth of tendril (up-curve) induced by indirect electric stimulation (Cucurbita).

on all sides. The specimen was held in a clamp, and the tip suitably attached to the recorder. For indirect stimulation, a feeble current from an induction coil was applied by two electric connections below the clamp. Direct stimulation was effected by sending the current through the length of the organ, the two electrodes being placed the one above and the other below the clamp (fig. 44).

Experiment 52. *Effect of indirect electric stimulation.*—The tendril was mounted on a Balanced Crescograph, the

indications of which give the immediate and the after-effect of stimulation. After securing exact balance, the record was horizontal. Indirect stimulation was now applied below the clamp, this upset the balance, shown by the resulting up-curve, which indicates a sudden acceleration of growth above the normal. This acceleration took place within 10 seconds of the application of stimulus and persisted for 3 minutes. The normal rate of growth then became restored, the record becoming once more horizontal (fig. 45).

FIG. 46. Variation of growth of tendril induced by direct electric stimulation.

First part of the curve shows normal rate of growth. Direct stimulation induced contraction (reversal of curve). After-effect of stimulation seen in highly erect curve in upper part of record, taken after 20 minutes (Cucurbita).

Experiment 53. *Effect of direct electric stimulation.*—The contraction induced by direct stimulation is so great that the record obtained by the sensitive method of balance cannot be kept within the plate. I therefore took a Crescographic record of the growth-curve without balance. The first part of the curve represents normal growth; stimulus of a feeble electric current was then directly applied near the highest point of the curve. This induced an immediate contraction and reversal of the curve, the contraction persisting for 2½ minutes; growth was then slowly renewed (fig. 46). The most interesting fact regarding the after-effect of stimulation is that the rate of

growth became greatly enhanced, even more than three times the normal. This is clearly seen in the record (upper half of the figure) taken 20 minutes after stimulation, the curve being far more erect than that of the normal rate of growth before stimulation.

The effects of indirect and direct electric stimulation of the tendril are, therefore, as follows:

1. Indirect stimulation induces sudden enhancement of the rate of growth, followed by recovery to the normal rate.
2. Direct stimulation induces a retardation of the rate of growth. *The after-effect of direct stimulation of moderate intensity is a short-lived enhancement of the rate of growth above the normal.*

I now proceed to show that mechanical stimulation induces effects which are very similar.

Effects of Direct and Indirect Mechanical Stimulation

Experiment 54. *Effect of direct mechanical stimulation.* I took a growing tendril of Cucurbita, and after taking a record of its normal rate of growth, subjected it to feeble mechanical stimulation by rubbing its different sides. The immediate effect was a retardation from the normal rate of 0·44 μ to 0·20 μ per second, the reduced rate being less than half the normal. The tendril recovered its normal rate of growth after the feeble stimulation; in fact, the effect after 15 minutes was even a slight acceleration above the normal, the growth-rate being 0·59 μ per second. The results are given in the following table:

Table XII.—The Immediate and After Effect of Mechanical Stimulation on Growth of Tendril (Cucurbita).

Normal rate of growth . .	0·44 μ per second
Retarded rate immediately after stimulation .	0·20 μ " "
Recovery and enhancement after 15 minutes .	0·59 μ " "

The effect of unilateral stimulation will be next considered.

EFFECT OF DIRECT UNILATERAL MECHANICAL STIMULATION

The previous experiment gives the effect of diffuse mechanical stimulation of the tendril. I now describe the effect of direct unilateral stimulation applied at the growing region.

Experiment 55.—The tendril of Cucurbita was mounted on the Balanced Crescograph, and the record obtained with a single recording lever. The first part of the curve shows

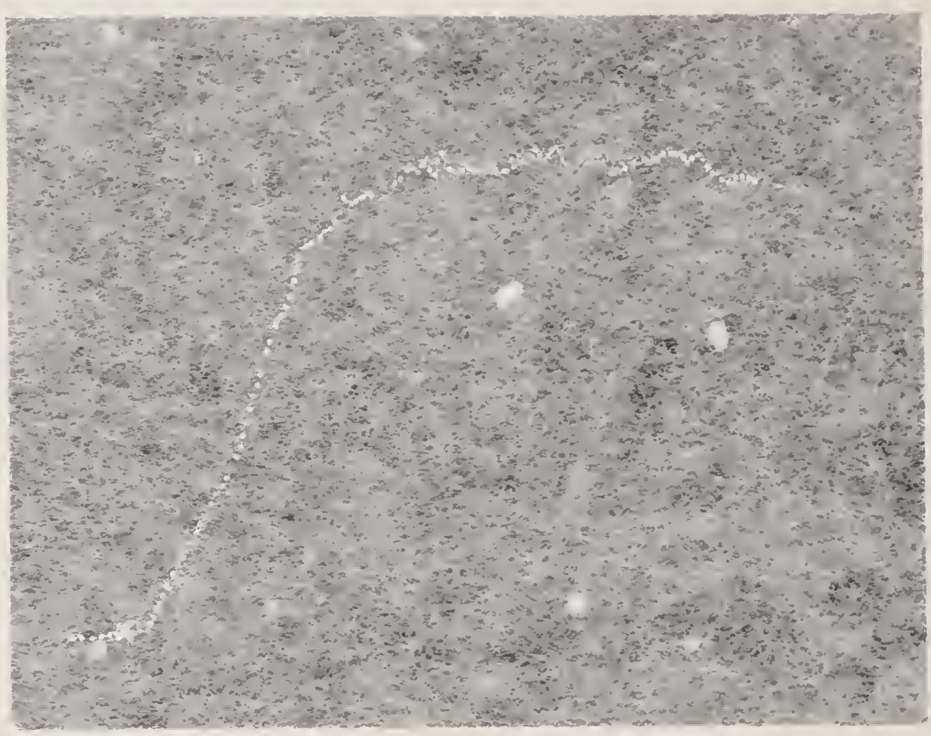


FIG. 47. Positive curvature of tendril of Cucurbita under stimulus of unilateral contact at X.

the horizontal record of balanced growth. Unilateral contact-stimulation was effected between two successive dots (which were at intervals of 3 seconds) with the object of not disturbing the record. Positive curvature was induced in the course of about 10 seconds and attained its climax in about 2 minutes, after which the tendril slowly recovered, as shown in the horizontal curve in the upper part of the record (fig. 47). Feeble stimulation is attended by a recovery within a short time. Under strong stimulation the curvature becomes more persistent.

Effect of Indirect Unilateral Mechanical Stimulation

Experiment 56.—A tendril of Passiflora was held in a clamp as in the diagram (fig. 48). The responsive movement of the tendril was observed by focusing a reading-microscope on a mark on the upper part of the tendril. Direct mechanical stimulation made the tendril move towards the stimulated side, the response being *positive*, as was also found in the last experiment. The stimulus was next transferred to a point below the clamp, but on the same side as before. This gave rise to a *negative* responsive movement, *i.e.* in a direction away from the stimulated side. This reversal into negative tropic curvature is due to the fact that the transmitted effect of indirect stimulation induces an acceleration of growth on the same side higher up, producing a convexity in the growing region.

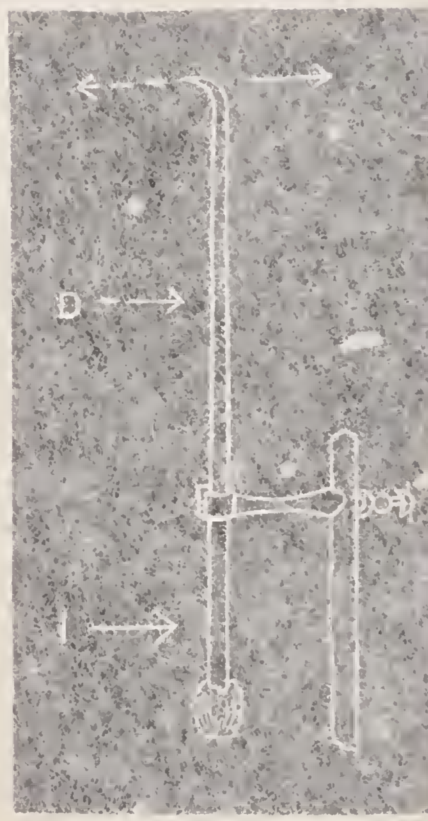


Fig. 48. Diagrammatic representation of effect of indirect and direct unilateral stimulation of a tendril (Passiflora).

Indirect stimulation I induces movement away from stimulated side (negative curvature), represented by continuous arrow above. Direct stimulation D induces positive curvature, indicated by dotted arrow above.

The different effects of direct and indirect unilateral stimulation are clearly indicated in the diagram (fig. 48).

Electric Response of Proximal and Distal Sides

The effects of unilateral stimulation on the two sides of the organ were next determined by the test of electric response, in which excitatory reaction is detected by electric change of galvanometric negativity, while expansive reaction is indicated by galvanometric positivity.

Experiment 57.—Taking a tendril, I made suitable electric connections for two series of experiments with an identical specimen. In the first, an electric connection

was made with the proximal side to the right (the proximal side being the side to be directly stimulated), the second connection being made with a distant indifferent point. Similar connections were also made for the second series, the two electric contacts being respectively made with a distal point diametrically opposite to the proximal, and with an indifferent point at a distance. A sensitive galvanometer was included in the electric circuit for record of the responses at the proximal and distal points.

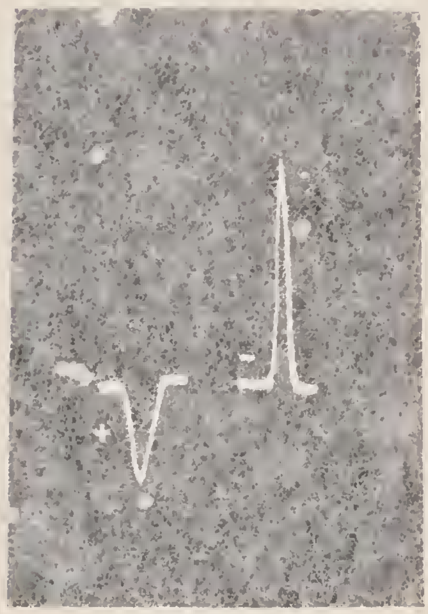


FIG. 40. Electric response at the distal and proximal sides of a tendril under unilateral mechanical stimulation.

Galvanometric positivity is induced at distal side (down curve), while galvanometric negativity (up-curve) is exhibited at the proximal side (Vitis quadrangularis).

Mechanical stimulation was effected by friction applied very near the proximal point. The record first taken was that of the effect on the distal side of this indirect stimulation. The down-record, followed by recovery, indicates a positive electric variation, indicative of increase of turgor, expansion and enhancement of growth at the distal point. Record was next taken of the effect of the direct stimulation on the proximal side. The larger up-response indicates strong galvanometric negativity, indicative of diminution of turgor, contraction and retardation of growth (fig. 40).

These phenomena of responsive reaction in the tendril will be shown to be by no means unique, but similar to those of other organs under all forms of stimulation. The only speciality in the tendril is that, owing to its structure, the perceptive power of the organ for mechanical stimulation is highly developed.

The following is a brief summary of the facts established in regard to the responsive characteristics of the tendril, and the tropic curvature induced in it by unilateral stimulation :

1. The proximal side contracts because it is directly stimulated, the expansion of the distal side being due to indirect stimulation. The curvature is brought about by the joint action of contraction on the one side and expansion on the opposite side.
2. The recovery of the tendril after brief stimulation is hastened by the after-effect of stimulation, which is an active expansion and enhancement of growth (*cf.* Experiments 53, 54).

The contraction of the directly excited side, and the expansion of the indirectly stimulated distal side of the organ, will explain Fitting's important observation [1] that in a unilaterally stimulated tendril there is (1) an acceleration of growth on the convex side, and (2) a contraction on the concave side. Fitting ascertained that the tendril became straightened by the renewal of active growth on the excited side.

Response of the Less Excitable Side of Tendril

It is generally supposed that in the tendril of Passiflora the upper side is devoid of moto-excitability. My experiments show, however, that direct stimulation does induce contraction and concavity of that side, though the actual movement is relatively feeble, as shown below.

Experiment 58.- Feeble stimulus of the same intensity was applied on the upper and under sides of the tendril alternately. Successive stimuli were rendered more or less uniform by the following device. A flat strip 1 cm. in breadth was coated 2 cm. of its length with shellac varnish mixed with fine emery powder. On drying, the surface became rough; the flat surface was then gently pressed against the area of the tendril to be stimulated, and quickly drawn sideways so as to rub the upper or the under side of the tendril in each experiment. Stimulation, thus effected, induced a responsive movement of both sides of the organ.

[1] Pfeffer, *ibid.* vol. iii. p. 57.

The extent of the maximum movement was measured by the microscope-micrometer. The following results were obtained with four different specimens:

TABLE XIII.—SHOWING THE RELATIVE INTENSITIES OF RESPONSE OF THE UPPER AND UNDER SIDES OF THE TENDRIL (PASSIFLORA).

Movement induced by stimulation of under side, A	Movement induced by stimulation of upper side, B	Ratio $\frac{B}{A}$
(1) 53 divisions	14 divisions	[illegible]
(2) 106 ,,	15 ,,	[illegible]
(3) 60 ,,	8 ,,	[illegible]
(4) 80 ,,	10 ,,	[illegible]

The upper side of the tendril is therefore not entirely devoid of moto-excitability, its power of contraction being about one-seventh that of the under side.

INHIBITORY ACTION OF STIMULATION

The following puzzling phenomenon was observed by Fitting in tendrils which are specially sensitive on the under side:

'If a small part of the upper side and at the same time the whole of the under side be stimulated, curvature takes place only at the places on the under side which lie opposite to the unstimulated regions of the upper side. The *sensitiveness* to contact is thus as well developed on the upper side as on the under side, and the difference between the two sides lies in the fact that while stimulation of the under side induces curvature, stimulation of the upper side induces *no visible result*, or simply inhibits curvature on the under side, according to circumstances.' [1]

It certainly seems to be anomalous that one side of the organ, apparently inexcitable, should inhibit the response of the opposite side. The results of my experiments already described afford a satisfactory explanation of this curious phenomenon of inhibition.

[1] Jost, *Lectures on Plant Physiology*, trans. by R. J. Harvey Gibson, p. [illegible] (Clarendon Press).

It has been shown that direct and indirect stimulation induce two opposite reactions: direct stimulation induces diminution of turgor, contraction and retardation of growth (*cf.* Experiments 53, 54, 55, 57); indirect stimulation induces, on the other hand, increase of turgor, expansion and enhancement of the rate of growth (*cf.* Experiments 54, 56, 57). The indirect stimulation is transmitted not only longitudinally, but also across the organ.

Applying these principles to the explanation of the anomalous case described by Fitting, the reason why only those points on the directly stimulated under or proximal side exhibit response which are opposite to corresponding unstimulated areas on the upper or distal side, would appear to be this: that the remaining unresponsive points on the under or proximal side are opposite to corresponding stimulated areas on the upper or distal side from which indirect stimulation is transmitted which has an inhibitory effect.

The effects of direct and indirect stimulation and the general mechanism of tropic curvature are treated of in greater detail in Chapter XII.

SUMMARY

The response of a tendril is in no way different from that of growing organs in general.

Mechanical stimulus directly applied induces incipient contraction, that is, retardation of the rate of growth, the effect being similar to those induced by other modes of stimulation.

Stimulus of contact or of friction induces a moderate retardation in the rate of growth. On the cessation of stimulation, the normal rate is restored within a short time.

Under unilateral mechanical stimulation of short duration, the directly excited proximal side undergoes contraction, the indirectly stimulated distal side exhibits the opposite reaction of expansion. The induced curvature is thus

due to the joint effects of the contraction of the one side, and the expansion of the opposite side.

As the after-effect of direct stimulation of moderate intensity is an acceleration of growth above the normal, the stimulated side undergoes an expansion by which the recovery is hastened.

Direct application of unilateral stimulus induces a *positive* curvature, but the same stimulus applied indirectly at a distance from the responding region induces a *negative* curvature.

The dorsiventral tendril of Passiflora is excitable on both the upper and under sides; the excitability of the under side is about seven times greater than that of the upper side.

Stimulation of one side of the tendril induces expansion of the opposite side, even in cases where the excitability of the stimulated side is feeble.

The response to direct stimulation of the more excitable side of the tendril is thus inhibited by stimulation of the opposite side, as seen in Fitting's experiment. This is a case of the neutralisation of the effect of direct by that of indirect stimulation.

CHAPTER XI

THE PHOTOTROPIC EFFECT OF LIGHT

LIGHT induces movements of an extremely varied character. Radial organs exhibit tropic movements in which the position of equilibrium is definitely related to the direction of the incident light. Such stems often bend towards the light, while roots, generally speaking, are supposed to bend away from it. It might be thought that this is due to a specific difference of irritability between shoot and root, the irritability of the former being of a positive, and of the latter of a negative, character. There are, however, numerous exceptions to this hasty generalisation.

The intensity of the light has a modifying influence on the character of the response. Thus, under unilateral photic stimulation of increasing intensity and duration, a radial organ may exhibit a positive, a dia-phototropic, and, finally, a negative response. Strong sunlight brings about a para-phototropic movement in which the apices of the leaves or leaflets turn towards or away from the source of illumination. The teleological argument advanced, that in this position the plant is protected from desiccation by transpiration, does not hold good universally; for under strong light the leaflets of *Cassia alata* assume a position by which the plant risks excessive loss of water.

An identical organ, as previously stated, may appear to exhibit sometimes a positive and at other times a negative response. Thus the leaflets of *Mimosa pudica* acted on by light from above fold up *towards* the light, the phototropic

effect being *positive*. But when the leaflets are acted on by light from below, then they also exhibit an upward folding, the phototropic effect being now *negative*. Precisely opposite effects are exhibited by the leaflets of Biophytum and Averrhoa. They fold downwards whether light acts from above or from below.

In these circumstances the hypothesis of the positive or negative irritabilities of different organs is quite untenable. Phototropic reactions are complex, for they represent the summated effects of numerous factors. The individual effect of these can only be ascertained by careful inspection of the curves of response recorded continuously under the action of light. The mechanism of tropic curvature will be dealt with in detail in the next chapter.

Positive Phototropic Curvature

In this chapter I describe:

1. The positive curvature of pulvinated and growing organs exposed to light.
2. Determination of the latent period.
3. The immediate and the after-effect of light.
4. The relation between the quantity of light and the responsive curvature.

I have already shown (p. 68) that there is no essential difference between the responses of pulvinated and those of growing organs, direct stimulation inducing contraction in both. The experimental investigation of the tropic effect of light has been carried out with both pulvinated and growing organs.

Phototropic Recorder

A very sensitive method had to be devised for obtaining accurate record of phototropic movements of pulvinated and of growing organs. The writing lever is made of fine glass fibre (fig. 50). The fulcrum-rod supported on jewel-

bearings has a small wheel (smaller than represented in the figure) to which is attached the leaf (upper figure) or the stem (lower figure). The up-movement of the leaf under

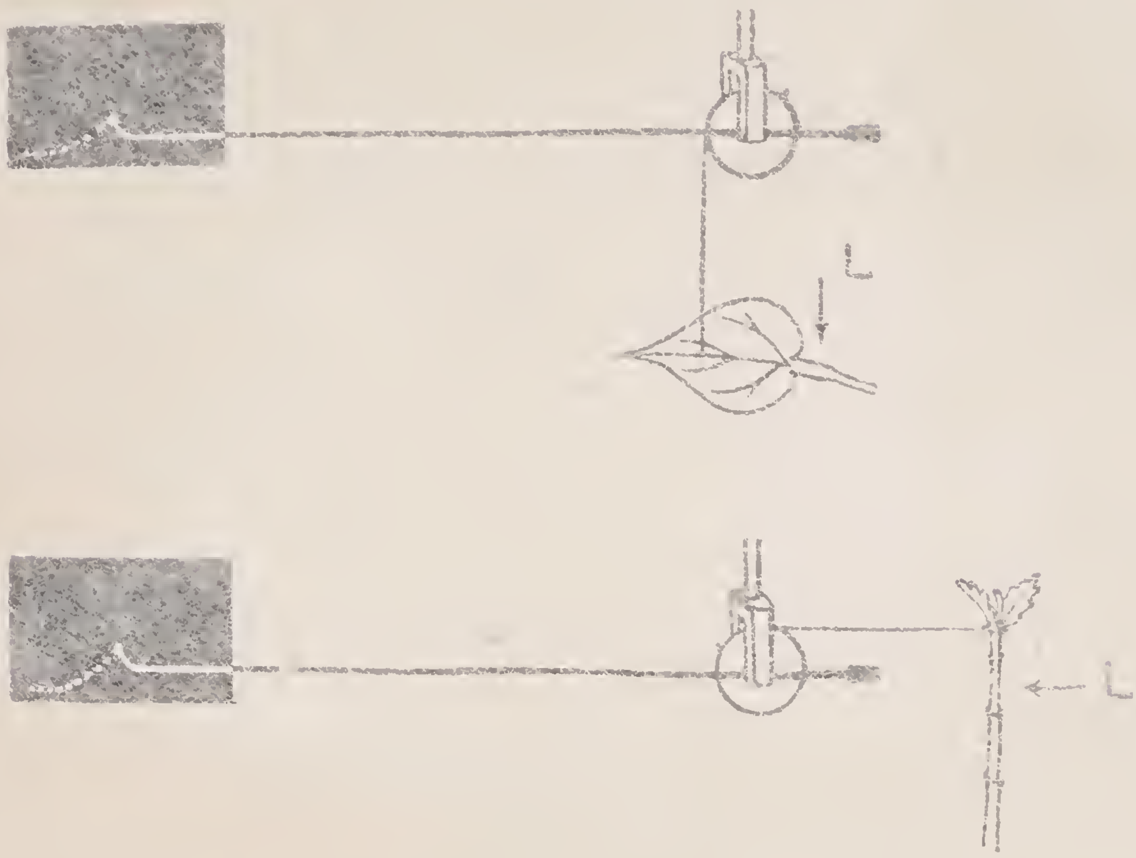


FIG. 50. The Phototropic Recorder: for pulvinated organ (upper figure), for growing organ (lower figure).

vertical light, or the bending of the stem in response to unilateral photic stimulation, is recorded as an up-curve on an oscillating smoked-glass plate.

Positive Phototropic Response of Pulvinated Organs

Experiment 59. *Response of pulvinated organs.*—For this experiment I employed the terminal leaflet of Phaseolus. The source of illumination was a 32-candle-power electric lamp, enclosed in a metallic tube with a circular aperture for passage of the light. The leaflet was attached to the Phototropic Recorder. Light was applied on the upper surface of the pulvinus for 20 seconds; this induced an up-movement of the leaflet, due to the contraction of the upper half of the

organ. Recovery took place in the course of 8 minutes (fig. 51). Similar effects were observed with the leaflets of

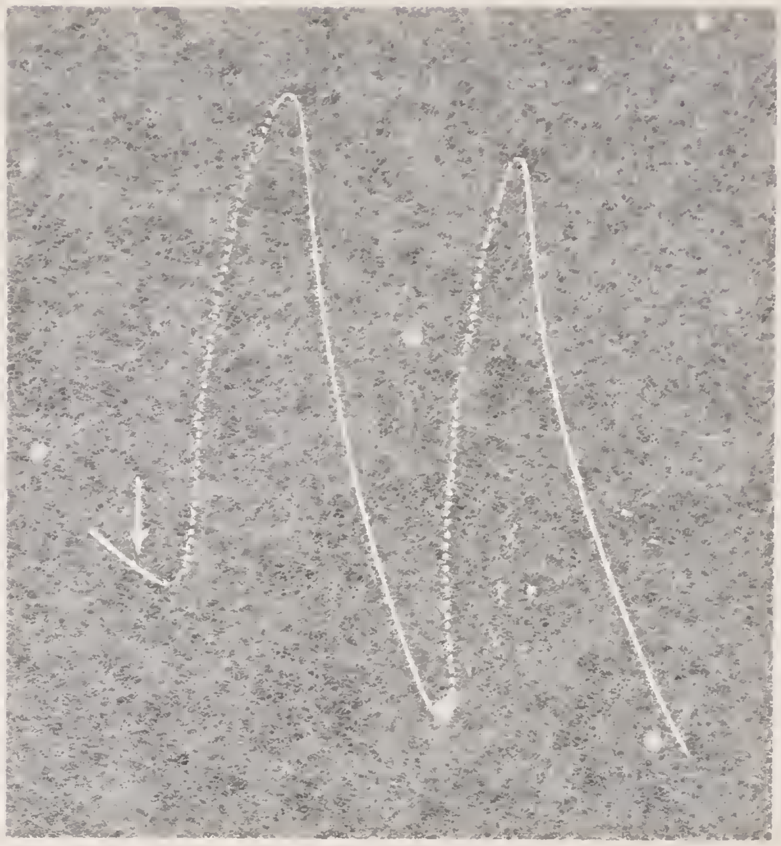


FIG. 51. Positive tropic effect of light on pulvinated organ. Responses to successive stimulations by light. Up-curve represents up-movement and down-curve represents recovery. (Phaseolus.)

Erythrina indica and of *Clitoria Ternatea*. The movement under light from above has for simplicity been described

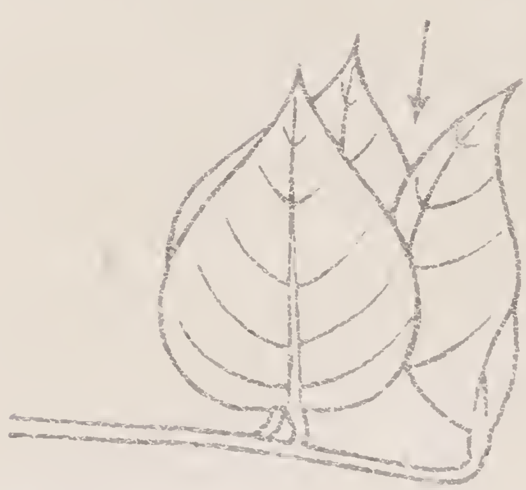


FIG. 52. Positive response of leaflets of Erythrina indica. (Para-heliotropic response.)

as upward. But the actual direction in which the leaflets point their apices is towards the source of light. Both these plants are so remarkably sensitive that the leaflets

follow the course of the sun in such a way that the axis of the cup, formed by the terminal and lateral leaflets, is coincident with the sun's rays (fig. 52).

Positive Phototropic Curvature of Growing Organs

For this I employed with success the young stems of numerous plants such as *Dregea volubilis*, *Vicia Faba*, and

Fig. 53. Positive phototropic curvature of a growing stem. Light applied at vertical arrow and withdrawn at horizontal arrow within circle. Successive dots at intervals of 10 seconds. (Vicia Faba.)

others. The reaction of some of these was relatively feeble and sluggish, whereas in others it was far more energetic.

Experiment 60. *Positive phototropic curvature of Vicia Faba.*—Light from a 25-candle-power Pointolite acted on one side of the young stem at the most active growing region, the record being taken on a smoked plate oscillating

once in 10 seconds. The moment of application of light is indicated by the up-pointing arrow, and its removal by the horizontal arrow within circle, the total duration of exposure being 60 seconds. It will be noted that the response occurred within a short time of the exposure, and that the tropic movement persisted for nearly 3 minutes after the cessation of light, when there was a recovery which was practically complete (fig. 53).

It may be said in general that there is a quick recovery after stimulation of moderate intensity and duration. But the curvature induced under stronger stimulation remains more or less persistent ; in extreme cases it becomes fixed by permanent growth.

Determination of the Latent Period

The latent period of phototropic response is usually regarded as of long duration, from several minutes to an hour or so. The shortest latent period for the cotyledon

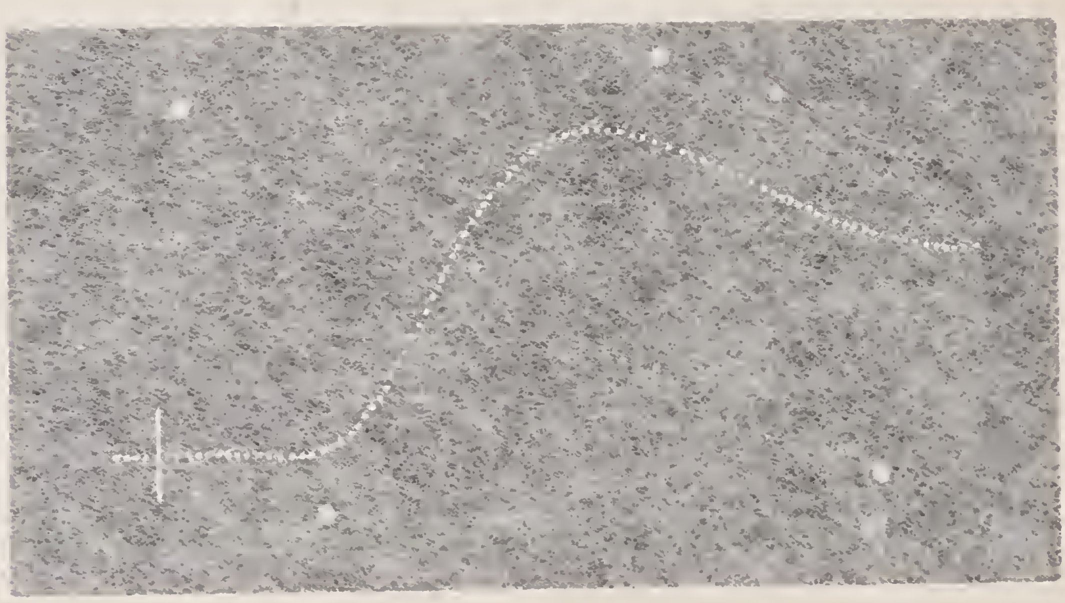


Fig. 54. Latent period of response to light in a pulvinated organ. Response occurred after 14 dots which were at intervals of 2 seconds. (Erythrina.)

of Avena was found by Czapek to be 7 minutes. Little is known about the relation of the latent period to the intensity of light.

Experiment 61. *Latent period of Erythrina*.—The recording plate was made to move at a fast rate, the successive

dots being at intervals of 2 seconds. Record of response was taken under moderate intensity of light acting from above, and the latent period was found to be as short as 28 seconds (fig. 54). Under the action of stronger light the latent period was further shortened. The latent period for retardation of growth under diffuse stimulation by light has also been found of the same order, namely, 35 seconds (*cf.* fig. 54).

Two different meanings are attached to the expression *latent period*. It may connote the interval between the application of stimulus and the initiation of response, being in the cases just described of the order of about 30 seconds; or it may be taken to mean the shortest period of exposure to stimulus for ensuring response. Taking the case of light it may well be asked what is the shortest exposure to light for inducing a retardation of growth in extremely sensitive plants? For this investigation I employed the highly sensitive method of the Balanced Crescograph.

Growth-Variation Caused by Flash of Light from a Single Spark

Experiment 62.—The duration of a spark-discharge from a Leyden jar is almost instantaneous, being of the order of $\frac{1}{1000000}$ of a second. A single discharge was made to take place between two small steel spheres, the light given out by the spark being most effective in retarding growth. The plant employed was a seedling of Wheat mounted on the Balanced Crescograph; after exact compensation of its normal growth, the record was horizontal. The spark gap was placed at a distance of 10 cm. from the plant, which was also illuminated from behind by reflected rays from a suitably inclined mirror. The flash of light from a single spark is seen to have induced a sudden retardation of the rate of growth, which lasted for 1½ minutes. The record shows another interesting peculiarity, namely, acceleration as an after-effect of moderate stimulation.

After the retardation, which lasted for 100 seconds, there was an acceleration of growth above the normal, persisting for 5 minutes, after which the rate of growth returned to normal (fig. 55).

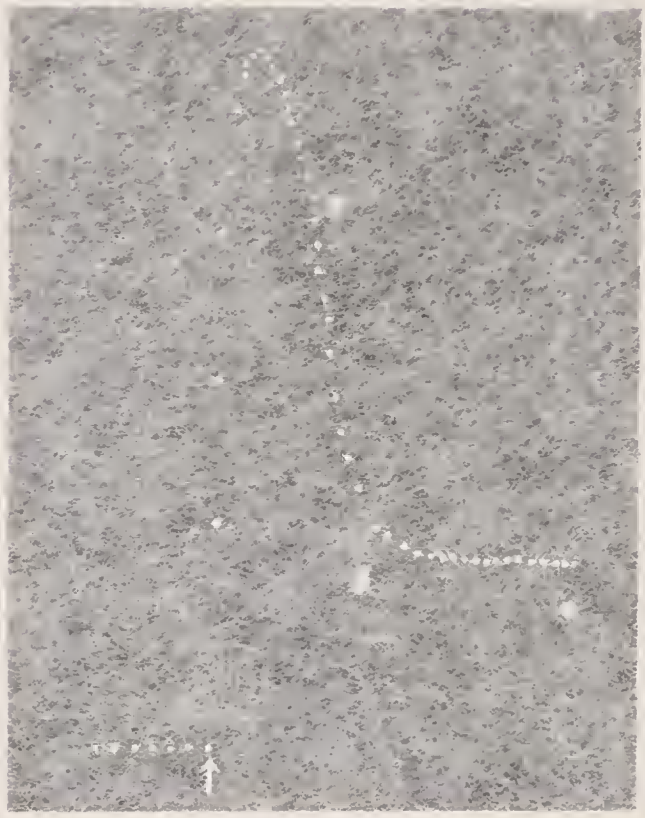


FIG. 55.—Effect of a single electric spark in causing variation of growth.

Record taken by Balanced Crescograph. Spark at arrow induced retardation of rate (up-curve); after-effect is acceleration above normal (down curve) followed by return to normal rate. (Wheat.)

In order to show that the induced variation is due to the action of light and not to any electric disturbance, I interposed a sheet of ebonite between the spark-gap and the plant; there was now no response when the spark passed.

Maximum Positive Curvature under Continued Action of Light

One important factor in the production of positive curvature is the contraction of the proximal side of the organ. The curvature becomes greater and greater with increasing contraction of that side. A limit of curvature is, however, reached because:

1. The contraction of the cells must have a limit;
2. The bending organ offers increasing resistance to curvature; and
3. The induced curvature tends to place the organ parallel to the direction of light, when the tropic effect is reduced to a minimum.

Relation between Quantity of Light and Induced Curvature

I now describe the effects of increasing intensity and duration of exposure to light on a pulvinated and on a growing organ. The pulvinus of the terminal leaflet of *Desmodium gyrans* was employed for the former, and a growing bud of Crinum for the latter.

Effect of Increasing Intensity of Light

Experiment 63. *Effect on pulvinus of Desmodium.*—A petiole bearing the terminal leaflet was suitably mounted in a **U**-tube filled with water. The wound-effect of section passed off in the course of an hour. Light of increasing intensity was successively applied from above, producing increasing contraction of the upper half of the pulvinus and increased up-movement of the leaflet, resulting in enhancement of the amplitude of response. The first record was obtained under light of a given intensity, and the second under an intensity twice as great (fig. 56). If tropic curvature increased in proportion to light-intensity, then the two responses would have been in the ratio of 1 : 2. The actual ratio was however slightly greater, namely, 1 : 2·6. It will be shown in a succeeding chapter,

FIG. 56. Tropic effect of increasing intensity of light, 1 : 2, on the positive response of terminal leaflet of Desmodium

that strict proportionality holds good only in the median range of stimulation, and that in a complete phototropic curve the *susceptibility* to excitation undergoes an increase at the beginning of the curve (p. 150).

The effect of light of increasing intensity on tropic curvature of growing organs will now be considered. Since

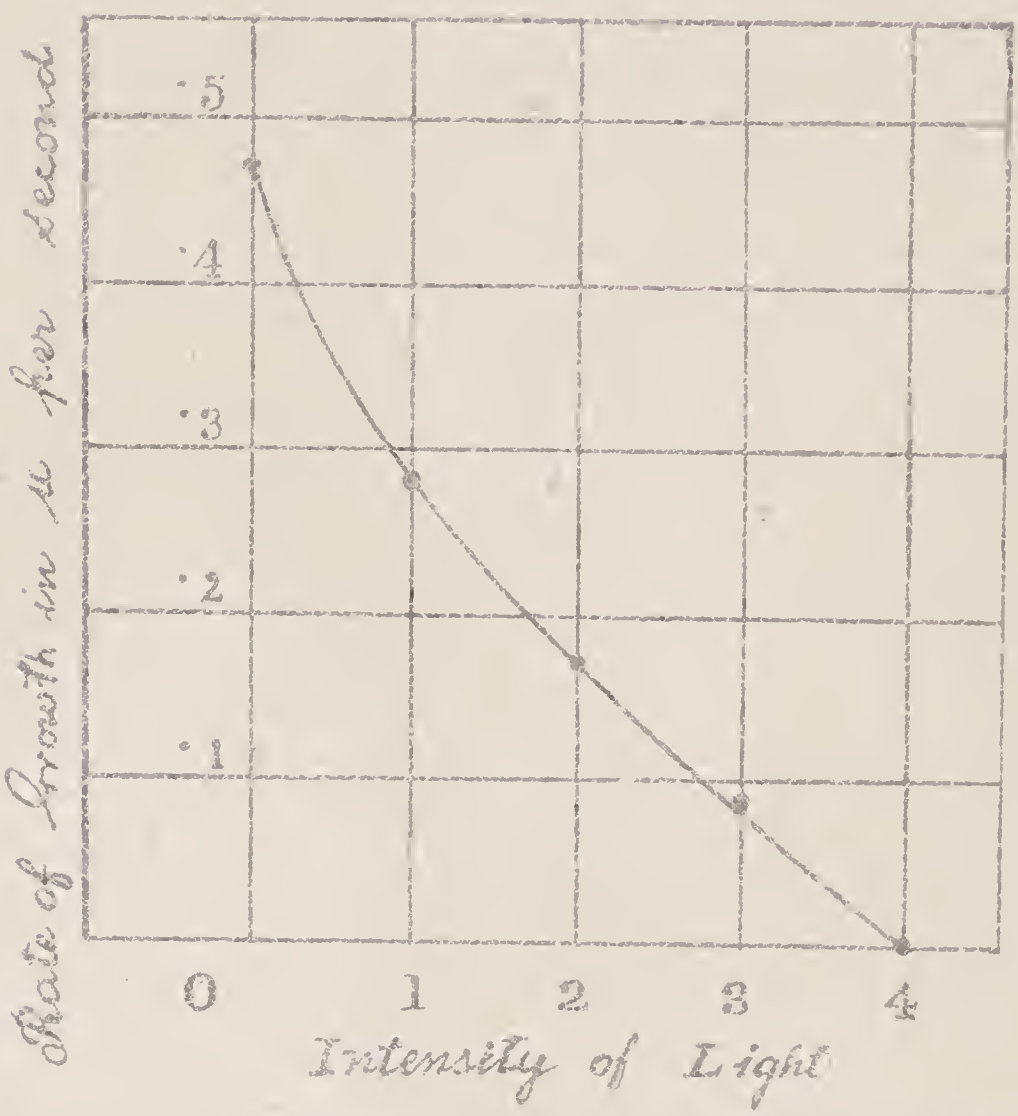


FIG. 57. Curve showing the relation between intensity of light and retardation of rate of growth (Crinum).

phototropic curvature is mainly due to one-sided retardation of growth, I will recapitulate the results previously obtained on the effect of light of increasing intensity on growth itself. The normal rate of growth of Crinum in the dark was 0·47 μ per second; this was reduced to 0·29 μ under the intensity of light of 1 unit, to 0·17 μ under 2, and to 0·09 μ under 3 units; growth became arrested when the intensity was raised to 4 units (p. 74). The curve of variation of growth under increasing intensity of light is

given in fig. 57 which shows that the retardation of growth is at first rapid and then tends to reach a limit. This must also be true when light acts only on one side of the organ, the retardation of growth of the directly stimulated proximal side of the organ contributing to bring about the positive curvature.

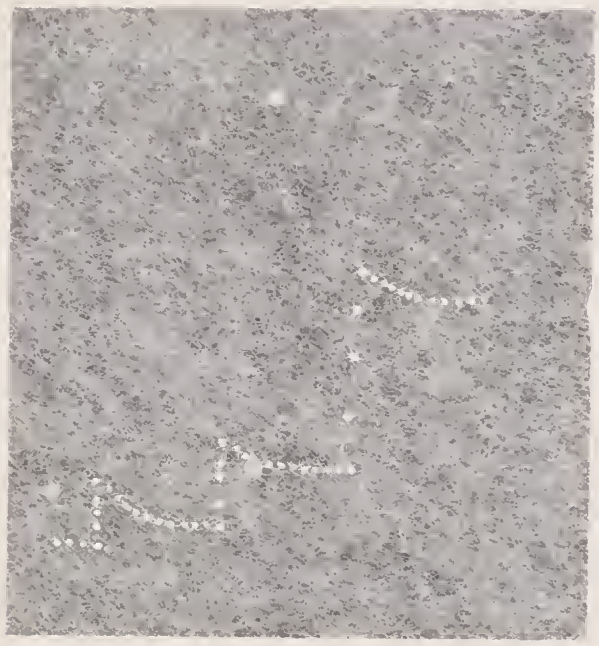


FIG. 58. Tropic effect of increasing intensity of light, 1 : 2 : 3, on growing organ (Crinum).

Experiment 64. *Tropic curvature of a growing organ.*—The flower-bud of Crinum was used for this experiment. The intensity of light acting on one side of the organ was increased by bringing the source of light nearer to it, the duration of exposure being in all cases kept the same, namely, 1 minute. Increasing intensity of light in the ratio of 1 : 2 : 3 gave rise to increasing positive curvature (fig. 58) in the ratio of 1 : 2·5 : 5.

EFFECT OF INCREASING DURATION OF EXPOSURE

Experiment 65.—The specimen of Crinum was in a slightly subtonic condition: the responses therefore were a short-lived negative preceding the normal positive. The duration of successive exposures was for 1, 2, and 3

minutes. The amplitudes of the responses are in the ratio of 1 : 1·25 : 5 (fig. 59).

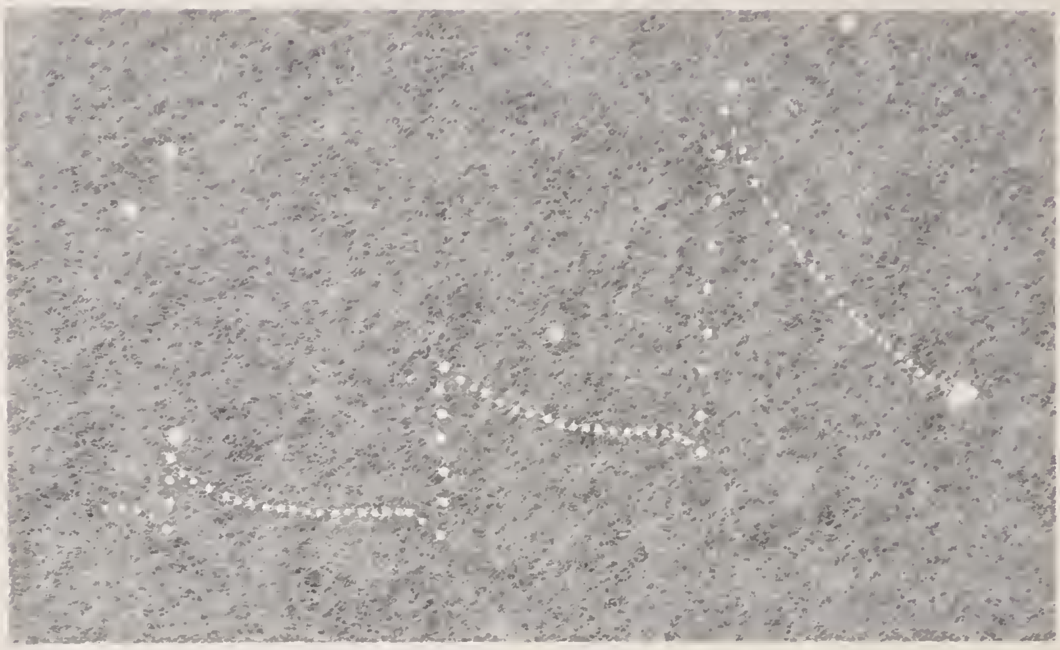


Fig. 59. Effect of increasing duration of exposure of 1 : 2 : 3 minutes on phototropic curvature of growing organ (Crinum).

Effect of the Angle of the Incident Light

The quantity of light which falls on a unit area of the responding organ varies as sin θ, where θ is the directive angle—*i.e.* the angle made by the rays with the surface. Some allowance has to be made for the loss of light reflected from the surface, this being greater at 45° than at 90°.

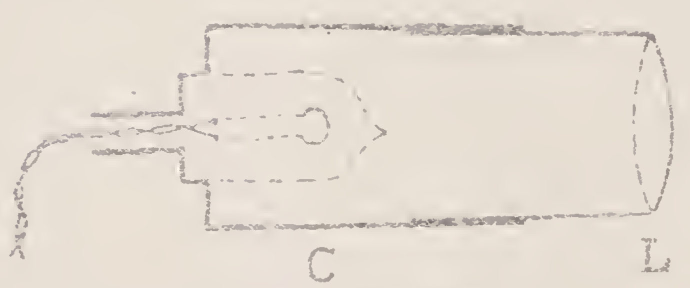


Fig. 60. The Collimator for application of light at various angles.

Experiment 66. *Response of a pulvinated organ.*—For application of light at various angles, an incandescent electric lamp was mounted at one end of a brass tube, a collimating lens being placed at the other end (fig. 60). The parallel beam of light from the Collimator could be thrown at various angles by rotating the collimator-tube round an axis at right angles to the tube. Light was directed for a minute, in the two successive experiments with the

pulvinus of Desmodium, at the angles of 45° and 90°. The record (fig. 61) shows that the phototropic effect increases with the directive angle. In the present case the ratio of the two effects is 1·6 : 1, which is not very different from the ratio $\frac{\sin 90^\circ}{\sin 45^\circ} = 1·4$.

Experiment 67. *Response of growing organs.*—A parallel experiment was carried out with the flower-bud of Crinum

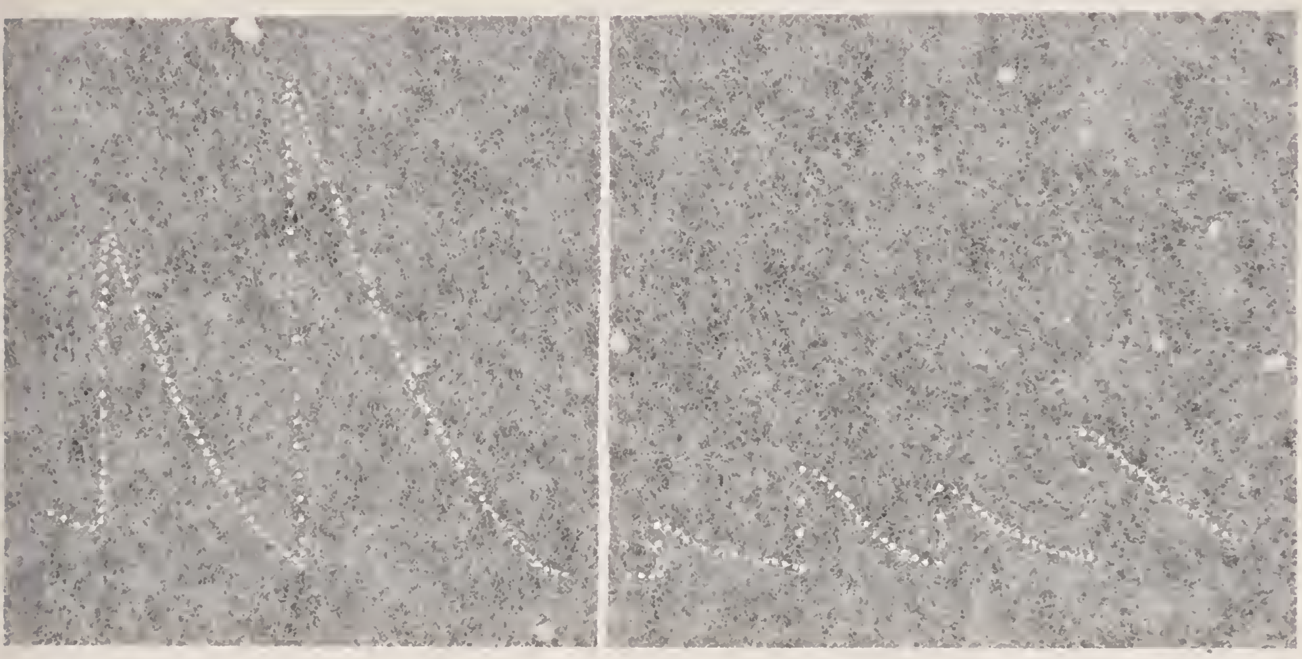


FIG. 61. FIG. 62.

FIG. 61. Effect of angle of incidence of light on tropic curvature of pulvinus of Desmodium.
The first response is to light at 45°, and the second at 90°.

FIG. 62. Records of tropic curvature of growing bud of Crinum on alternate stimulation by light at 45° and at 90°.

held vertical. Unilateral light was applied alternately at 45° and 90° in two successive series. It may be said in general that the excitability of a tissue in a condition slightly *below par* is increased by previous stimulation. From the series of responses obtained under alternate stimulation at 45° and at 90° it is possible to ascertain whether any variation of excitability had occurred during the course of the experiment, in order to make allowance for it. The records show that stimulation did enhance the excitability of the organ to a small extent. Thus the first stimulation at 45°

induced an amplitude of response of 5 mm.; the second stimulation at 45°, i.e. the third response of the series induced a slightly larger response 7 mm. in amplitude. Similarly the two responses at 90° gave amplitudes of 9 and 11 mm. respectively (fig. 62). Taking the mean value of each pair, the ratio of tropic effects for 90° and 45° is = 10/6 = 1·7, nearly—a value which is slightly greater than the ratio of the sines of the two angles.

The tropic effect of light as affected by increasing intensity, duration, and change of directive angle, may now be recapitulated: (1) the tropic effect is enhanced under increasing intensity of light; (2) it is increased with the duration of exposure; and finally (3) it is increased with the directive angle from grazing to perpendicular incidence. Taking into consideration the effects of these different factors the conclusion is that the phototropic effect increases with the quantity of incident light. It will be shown in a subsequent chapter that strict proportionality of cause and effect holds good only in the median range of stimulation, and the slight deviation from this is due to the fact that the *susceptibility* for excitation is feeble below that range.

SUMMARY

Phototropic response is similar in pulvinated and in growing organs.

One important factor in positive curvature is the contraction of the directly stimulated proximal side of the organ. The modifying effect of another factor will be described in the next chapter.

The induced curvature is followed by complete recovery after brief stimulation by light. The recovery is hastened by an acceleration of the rate of growth above the normal of the previously stimulated side. The recovery is prolonged after strong and long-continued stimulation.

The latent period for phototropic reaction is very much shorter than has been previously supposed. In certain

plants it is only about 30 seconds instead of minutes. The latent period is shortened under increased intensity of light.

The shortest period of exposure necessary to induce responsive contraction under the action of light is extremely short in certain cases. The seedling of Wheat responded to a flash of light from an electric spark, the duration of which is about a hundred thousandth part of a second.

Tropic curvature increases with the intensity and duration of exposure to light. It also increases with the directive angle, the effect being approximately proportional to sin θ, where θ is the angle made by the rays with the surface of the responding organ.

Within the median range of stimulation the intensity of induced tropic effect is proportional to the quantity of incident light.

CHAPTER XII

THE MECHANISM OF PHOTOTROPIC CURVATURE

Attention was mainly directed in the previous chapter to the effect of direct stimulation on the proximal side of the organ. It was shown that the positive phototropic curvature is attributable to the contraction of the stimulated side.

The question now arises whether the stimulus of light, acting on the proximal side of the organ, also induces a reaction at the distal side; if so, whether this helps or opposes the positive curvature. It has been shown in a previous chapter that unilateral mechanical stimulation induces not only contraction and retardation of growth of the proximal side, but also expansion and acceleration of growth of the distal side, the resulting curvature being due to these conjoint effects.

Does photic stimulation induce effects parallel to those produced by mechanical stimulation? And what are the effects, if any, of the impulse transmitted from the stimulated to the unstimulated side?

The Effects of Direct and Indirect Stimulation

In order to analyse the effects of stimulation, it has been necessary to devise a number of independent methods of investigation, the concordant results of which lead to a convincing conclusion. The questions to be answered are: Is the effect of stimulation to generate a single impulse or two impulses? Is the impulse modified in transmission by

the distance traversed and by the conducting capacity of the tissue? To these questions an answer is obtained from the study of the effects of Direct and Indirect Stimulation: by *Direct* stimulation is implied application of stimulus at or near to the responding organ; by *Indirect* stimulation, application of stimulus at some appreciable distance from the responding organ.

Direct stimulation.—Taking the case of an excitable shoot of Mimosa, direct stimulation of the pulvinus of a leaf at once causes it to fall. The same effect is produced when the stimulus is applied to the petiole, for the petiole is a fairly good conductor.

Indirect stimulation.—Continuing the experiment with the identical shoot, the same stimulus is now applied to the stem, with the result that, instead of falling as previously, the nearest leaf shows an erectile movement, which may or may not be followed by a fall.

These different effects suggest that stimulation generates, in the stimulated tissue, two impulses. The one, which induces the fall of the leaf, has been shown to be excitatory, that is, of the nature of protoplasmic excitation, and since the response which it evokes is designated *negative*, so the impulse itself may conveniently be termed negative also. The other, which induces the rise of the leaf; that is a *positive* response, may likewise be termed the positive impulse. But what is its nature? On grounds which have been fully discussed in previous works, more especially in the 'Ascent of Sap' (p. 247), I have come to the conclusion that it is an *hydraulic* impulse, of the nature of a wave of increased hydrostatic pressure which, originating in the contraction of the cells at the point of stimulation, travels to the pulvinus, causing it to expand. The two impulses produce opposite effects: the excitatory *nervous* impulse causes contraction of the responding cells, and is attended by galvanometric negativity: the *hydraulic* impulse causes expansion of the cells, and is attended by galvanometric positivity. Moreover, the hydraulic impulse resulting from stimulation

travels considerably faster than the nervous, and is not dependent upon the conducting power of the tissues in which it travels.

There are thus two distinct impulses initiated by stimulation, the universality of which is demonstrated:

1. By the identical effects induced by modes of stimulation so diverse as thermal, electric, and photic;
2. By the longitudinal and the transverse transmission of two impulses generated by stimulation;
3. By the opposite reactions induced in growing organs by the two impulses; and
4. By the electric detection of the two impulses.

It is necessary to explain here that it is not the stimulus but its effect that is transmitted to a distance. The phrase *transmission of stimulus* has, however, come into general use, and will be occasionally employed in the place of the more correct phrase *transmission of impulse*.

These points are well illustrated in the following experiments. Compared with that of the petiole, the conducting power of the stem of Mimosa is relatively feeble, as evidenced by the fact that the velocity of transmission of excitation is only 2 mm. as against 30 mm. per second in the petiole. The semi-conductivity of the stem makes it easier to obtain records of the effects of the two impulses.

Experiment 68. *Longitudinal transmission of impulse under radio-thermal stimulation.*—The method of experimentation is illustrated in fig. 63. The distance of the point of application of stimulus on the stem from the responding leaf was, in successive experiments with an identical specimen, reduced from S to S_1 and finally to S_2. The application of stimulus at a point opposite to the indicating leaf is represented by S_3. The radio-thermal stimulus of moderate intensity was kept constant, the intervening distance in successive experiments being reduced from 80 mm. to 30 mm., and finally to 10 mm. The record was taken on a fast-moving plate, the successive

dots being at intervals of a second. The resulting resp
given in fig. 64 should be read from below upwards.

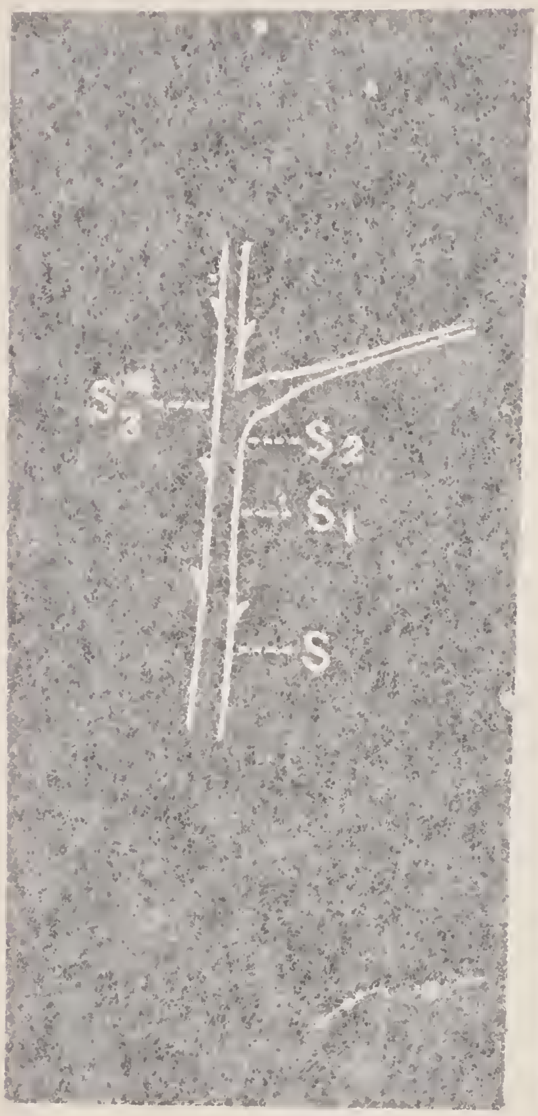


FIG. 63.

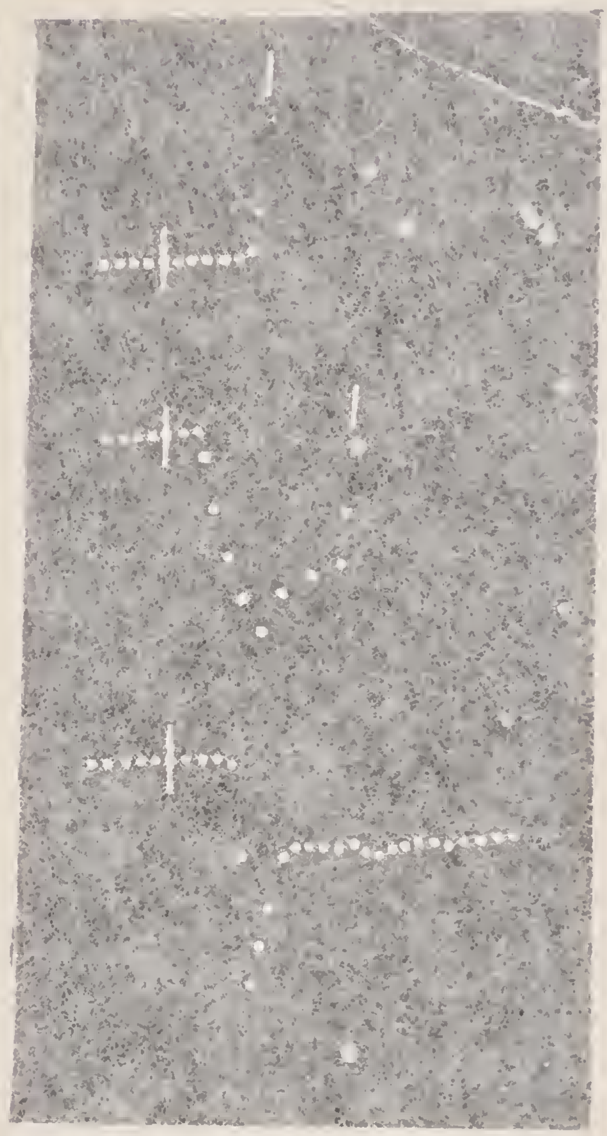


FIG. 64.

FIG. 63. Longitudinal transmission of impulse in stem of Mimosa.

Stimulus successively applied at S, S_1 and S_2. Transverse application of stimulus indicated by S_3.

FIG. 64. Records of effect of longitudinal transmission of impulse, to be read from below upwards.

Positive, diphasic and negative response to stimulation at S, S_1 and S_2. Erectile response in this and in the following represented by a down-curve, responsive fall being indicated by an up-curve. Successive dots at intervals of a second.

I first applied the stimulus S at a distance of 80 mm.; the transmitted impulse gave rise only to a positive *erectile* movement of the leaf followed by partial recovery, there being no *negative* response of the fall of the leaf. The

positive response occurred after an interval of 3·5 seconds; the failure of the negative impulse to reach the pulvinus may be ascribed to the feeble conductivity of the stem.

Stimulus was now applied at S_1 at a distance of 20 mm. The response was positive, an erectile movement of the leaf; this was followed by the excitatory negative, a rapid fall of the leaf as indicated by the scratch-line in the up-curve. The positive response was initiated after an interval of 2 seconds, while the negative occurred after 10 seconds. The velocity of the positive impulse under indirect stimulation is thus greater than that of the excitatory negative impulse of 2 mm. per second, obtained by dividing the distance of 20 mm. by the interval of time, 10 seconds.

Finally, the stimulus was applied at S_2 at a distance of 10 mm. from the pulvinus. The response was now only excitatory negative, which was initiated after 5 seconds, the velocity of conduction being the same as before, namely, 2 mm. per second. The positive response is here masked by the more intense excitatory negative reaction.

The results afford a basis for a rational explanation of various tropic movements, which is only possible by taking account of the two impulses, the existence of which is fully established.

Experiment 69. *Impulse under indirect electric stimulation.*—Exactly parallel effects were obtained under electric stimulation—that is to say, the response was positive when the stimulus was applied at a relatively long distance; a diphasic response, positive followed by negative, occurred when the stimulus was applied at a short distance. Application of stimulus at or near the responding organ gave rise only to negative response.

I will next show that similar positive and negative responses are obtained when the stimulus is applied on one side of the stem, the transmission being now in the transverse instead of in the longitudinal direction.

Transverse Transmission of Impulse

Of greater importance is the transverse transmission of impulse from the proximal to the distal side. It is obvious that the conductivity across the stem must be very much less than that along its length. Hence application of stimulus to the stem of Mimosa diametrically opposite to the indicating leaf, is equivalent to indirect stimulation of that leaf. I will describe the effects of photic, electric, and radio-thermal stimulation which result from the transmission of impulse across the semi-conducting stem.

Experiment 70. *Transverse transmission of impulse under photic stimulation.*—A narrow beam from a small arc-lamp was made to fall on the stem, at a point diametrically opposite to a motile leaf which was attached to the recording lever, the successive dots in the record being at intervals of a second. Stimulation by light caused a positive or erectile movement of the leaf indicator within 5 seconds of application. The positive response affords conclusive proof of the induction of increase of turgor at the distal point of the stem to which the leaf was attached. When the stimulus is moderate or of short duration the response remains positive. But under strong or prolonged stimulation the leaf falls, showing that the slower excitatory negative impulse is conducted to the distal point (fig. 65). It will be noted that the fall is slow at the beginning; it then becomes suddenly rapid, as indicated by a scratch-line instead of a dot in the record.

The excitatory impulse reached the motile pulvinus 35 seconds after the initiation of the positive response. The velocity of the negative impulse, it should be remembered, depends on the intensity of the stimulus; the stimulus was moderately strong and the stem was thin, only 2 mm. in diameter. The velocity of the excitatory impulse in the transverse direction in this case was 0·05 mm. per second.

Experiment 71. *Transverse transmission under electric stimulation.*—In order to show that the effects described

are not due to any particular mode of stimulation but to stimulation in general, I carried out the following additional experiments. Two fine pin-electrodes were inserted 5 mm. apart into the stem of Mimosa exactly opposite to the particular responding leaf. After a suitable period allowing for recovery from mechanical irritation, a tetanising

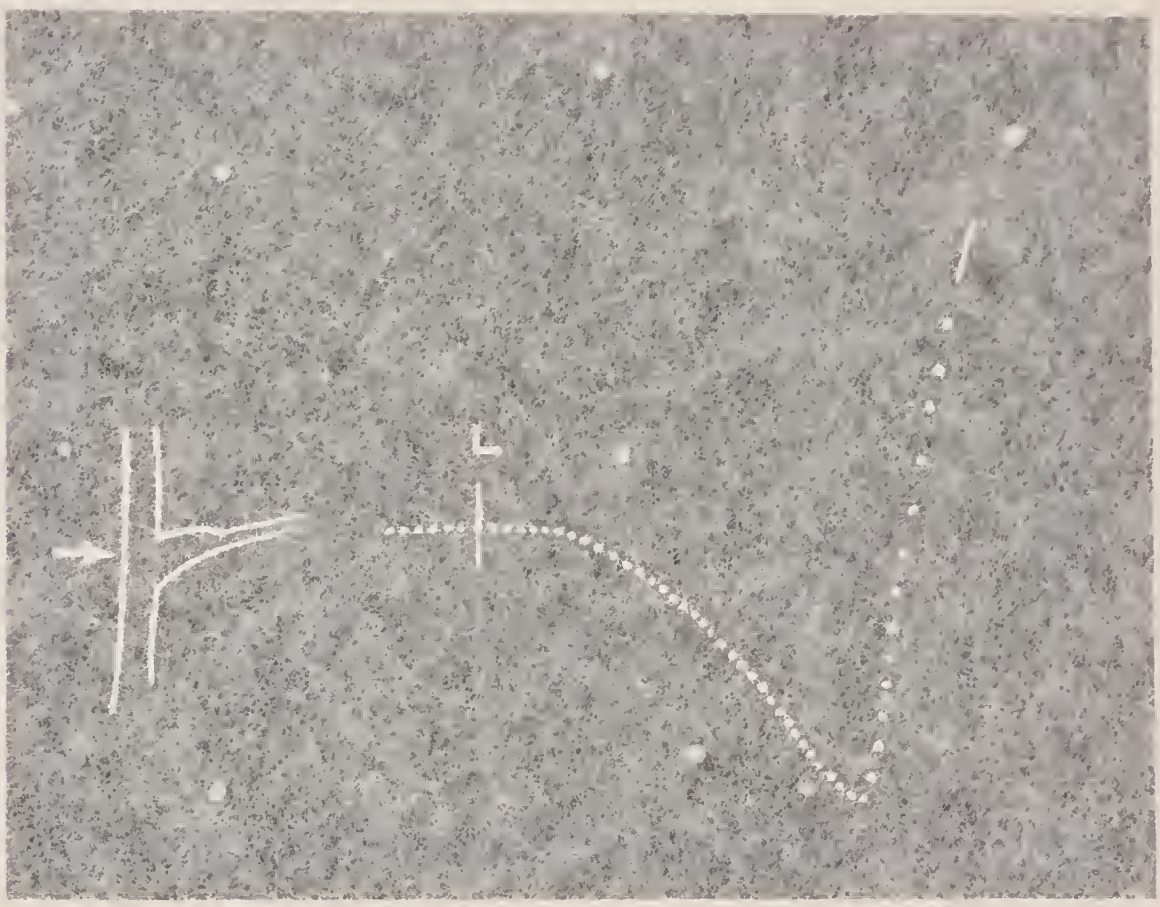


FIG. 65. Effect of transverse transmission of impulse under photic stimulation. Preliminary erectile response due to positive impulse (down-curve), followed by fall of leaf (up-curve) due to transverse conduction of excitation. (Mimosa.)

electric current of moderate intensity was passed through the electrodes. The responsive effects on the distal side of the stem were precisely similar to those induced under unilateral photic stimulation—that is to say, the first effect was an erectile movement of the leaf brought about by the positive hydraulic impulse; the excitatory negative impulse then reached the distal side after an interval of 31 seconds and caused a fall of the leaf (fig. 66). The velocity of conduction of excitation was 0·06 mm. per second.

Experiment 72. *Transmission under radio-thermal stimulation.*—Application of radio-thermal stimulus gave rise to results essentially similar. The intensity of stimulation was relatively stronger, and the negative excitatory impulse reached the distal side (after the hydraulic positive) in the course of 25 seconds (fig. 67), the velocity of the impulse being 0·08 mm. per second.

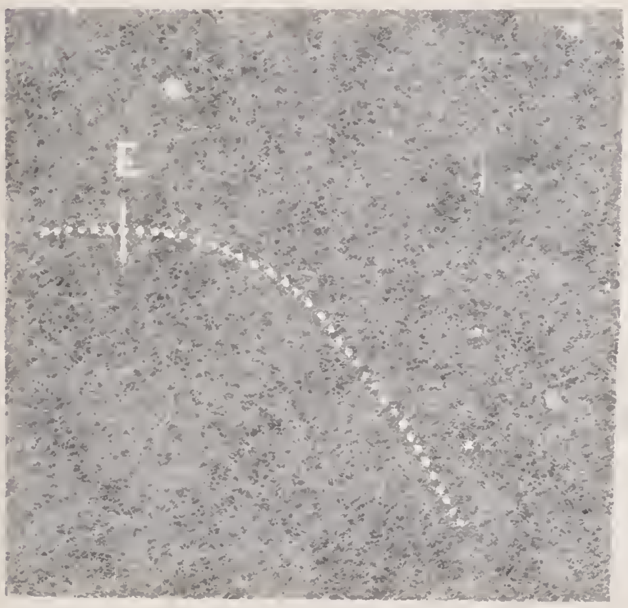


FIG. 66.

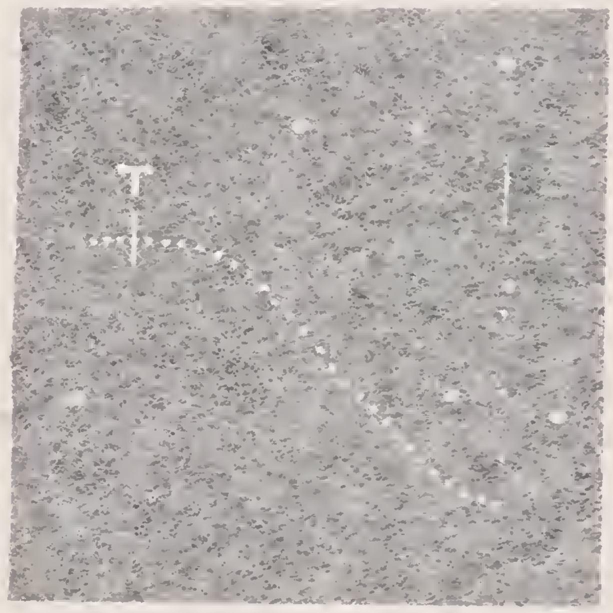


FIG. 67.

FIG. 66. Effect of transverse transmission of impulse under electric stimulation E.

FIG. 67. Effect of transverse transmission of impulse under radio-thermal stimulation T.

Note parallel effect exhibited in figs. 65, 66, 67; also slow fall of leaf in the commencement becoming suddenly rapid, as shown by the scratch line. (Mimosa.)

The experiments that have been described are of much significance. A rigid organ like the stem of Mimosa may appear insensitive to stimulation, since it exhibits no responsive movement; but its perception of stimulus is shown by its power of initiation and transmission of two characteristic impulses to a distance, one of which is the positive giving rise to an enhancement of turgor at the distal side, and the other the true excitatory negative inducing the opposite effect of diminution of turgor. Unilateral stimulation gives rise to both these effects in all organs—pulvinated, growing and non-growing. It is the

fortunate fact of the existence of the motile leaf of Mimosa that makes possible the most convincing demonstration of the reactions underlying the mechanics of tropic curvature.

To recapitulate: Stimulation gives rise to dual impulses, positive and negative; of these the positive impulse is not entirely dependent on the conducting power of the tissue, but the propagation of the excitatory negative impulse is greatly dependent on the conducting power. No tissue is a perfect conductor, nor is any a perfect non-conductor of excitation, the difference being a question of degree. A semi-conducting tissue, on feeble stimulation, will transmit only the positive impulse; on strong or long-continued stimulation it will transmit both positive and negative impulses, the positive preceding the negative. The transmitted positive gives rise to increase of turgor and expansion; the negative induces the opposite reaction of diminution of turgor and contraction.

In cases where transverse conductivity is feeble, the impulse transmitted to the distal side (indirect effect of stimulation) is positive, while the directly stimulated proximal side is negative. The tropic curvature is in such cases *positive*, being brought about as the conjoint effect of contraction of the proximal and expansion of the distal side. It is only under strong and long-continued stimulation that the excitatory negative impulse reaches the distal side, and may thus neutralise the positive curvature. Consideration of this aspect of the subject is deferred to the next chapter.

Effects of Direct and Indirect Stimulation on a Growing Organ

The characteristic effects of direct and indirect stimulation have been definitely established by experiments carried out with Mimosa. It has been shown that direct stimulation induces contraction and diminution of turgor, while indirect stimulation induces the opposite reaction of expansion and increase of turgor. What are the effects

of these reactions on a growing organ? Diminution of turgor has been shown to induce a retardation of growth, the incipient contraction culminating in a marked contraction (pp. 67, 68, 74). Enhancement of turgor due to indirect stimulation, on the other hand, has been shown to induce expansion and acceleration of growth (p. 91). The following experiments were so devised that the growing organ should itself record the responsive variations of growth under direct and indirect stimulation.

Experiment 73. *Effect of direct and indirect radio-thermal stimulation.*—The experimental specimen was a flower-bud of Crinum, held by a clamp a little below the region of growth (*cf.* fig. 48). Radio-thermal stimulus was applied below the clamp, so that the transmitted impulse had to pass through the securely held intervening tissue. The stimulus was unilaterally applied at a point about 50 mm. below the region of active growth. The first stimulation was feeble, and brought about an acceleration of growth on the same side with expansion and convexity, the resulting movement being *negative*, or away from the stimulus; this effect is attributable to the positive impulse transmitted to the region of growth. The latent period was 5 seconds, and the maximum negative movement was completed in the further course of 10 seconds, after which there was a recovery in the course of a minute and a half. A stronger stimulus S′ gave a larger response; but when the intensity was raised still higher to S″, the positive was overtaken by the excitatory negative impulse within 15 seconds of the commencement of the positive response; the convex was then succeeded by a concave curvature, the response being therefore diphasic (fig. 68). When the stimulation was direct, that is, applied at or near the region of growth, the response was a curvature towards the stimulus.

I will briefly summarise the results obtained with growing organs under direct and indirect stimulation. The effect induced by feeble stimulus applied at a distance from the growing region is a positive variation or acceleration of

growth: the effect is negative, i.e. retardation of growth, when the stimulus is applied at the responding region of growth; under intermediate conditions, the growth-variation is diphasic, positive acceleration followed by negative retardation.

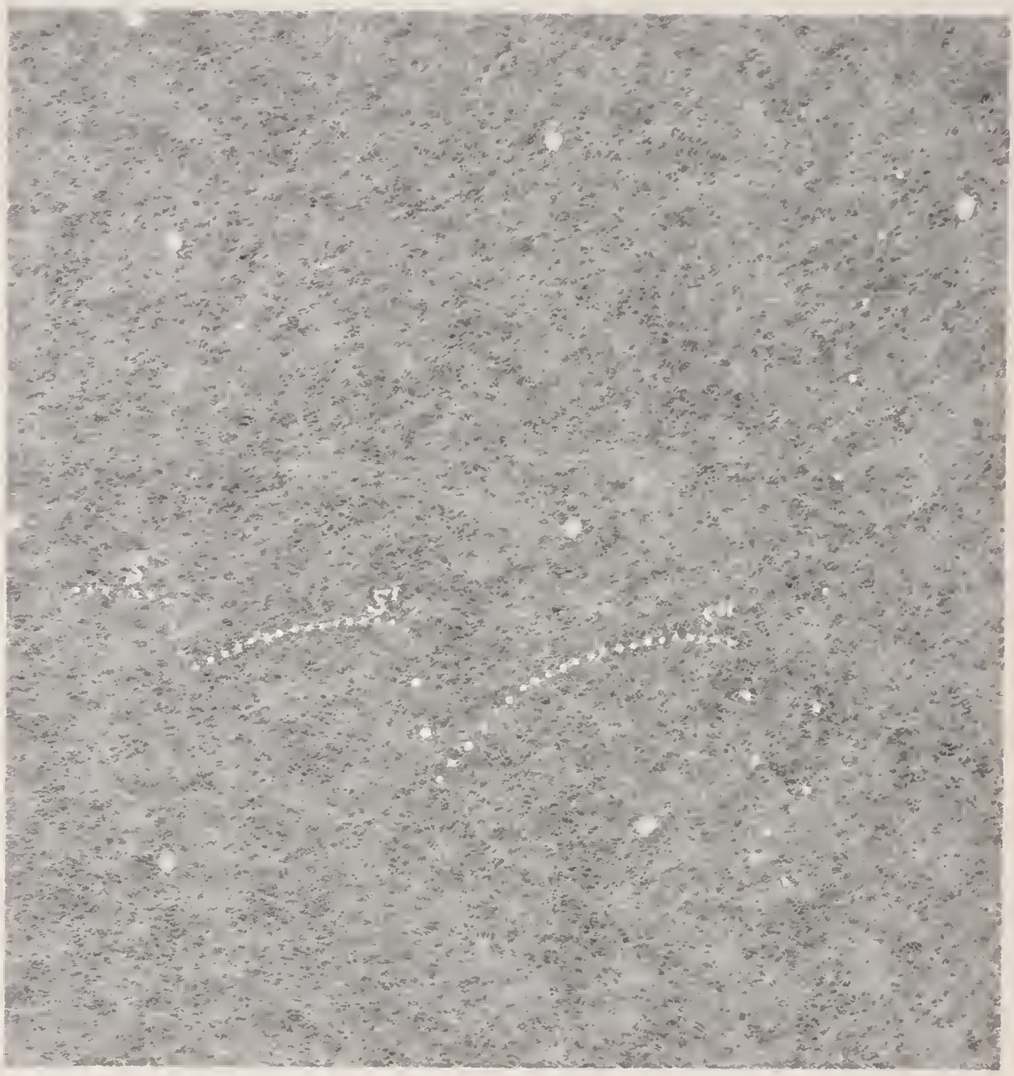


FIG. 68. Effect of indirect unilateral stimulation.

s, s', induced negative tropic effect (movement away from stimulated side): stronger stimulus s'' gave rise to negative followed by positive. (Crinum.)

Experiment 74. *Effects of indirect and direct electric stimulation.*—In the place of radio-thermal, I next applied electric stimulation. Taking a growing bud of Crinum I determined the region of its active growth; lower down a region was found where the growth had practically disappeared and could therefore be regarded as an indifferent region. In order to observe the effect of indirect stimulation on the rate of growth, I applied two electrodes on this

indifferent region about 1 cm. below the region of growth On application of diffuse and moderate electric stimulation of short duration, the response was an acceleration of growth

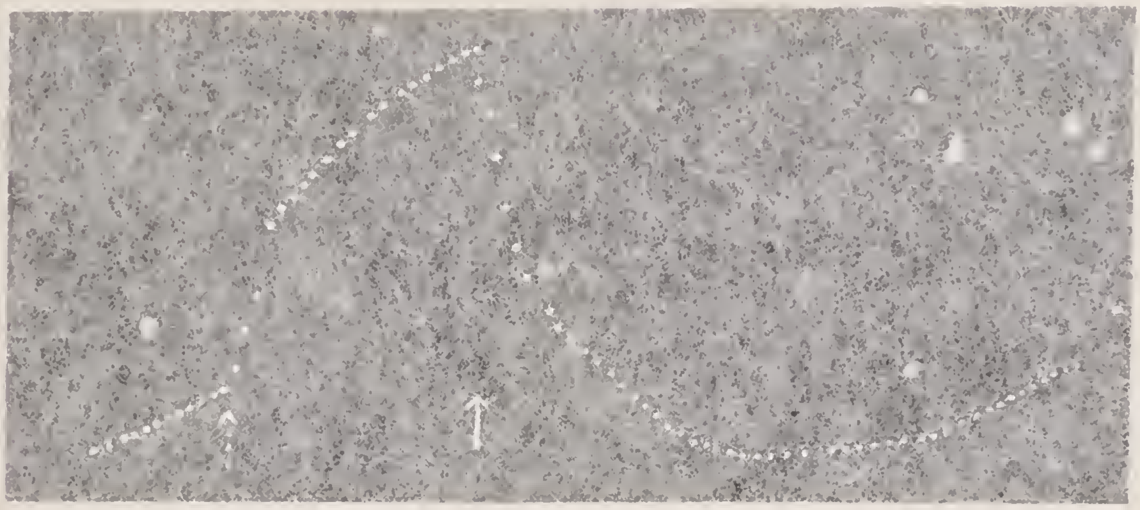


FIG. 69 Effect of indirect and direct electric stimulation on growth of Crinum, taken on a moving plate.

Dotted arrow shows the indirect application of stimulus, with consequent acceleration of growth (highly erect curve). Direct application of stimulus at the second arrow induced retardation of rate of growth which culminated in actual contraction (down-curve). Successive dots are at intervals of 5 seconds. (Magnification 2000 times.)

which persisted for nearly a minute, after which there was a resumption of the normal rate of growth. In this particular case the interval of time between the application of stimulus

TABLE XIV.—ACCELERATING EFFECT OF INDIRECT STIMULATION ON GROWTH (CRINUM).

Specimen	Condition of experiment	Rate of growth
No. I.	Normal After indirect stimulation	0·21 μ per second 0·26 μ ,, ,,
No. II	Normal After indirect stimulation	0·25 μ per second 0·30 μ ,, ,,

and the responsive acceleration of growth was 12 seconds. The interval varies in different cases from 1 second to 20 seconds or more, depending on the intervening distance between the point of application of stimulus and the responding region of growth. I give a record (fig. 69) obtained

with a different experiment which shows, in an identical specimen, (1) an acceleration of growth under indirect and (2) a retardation of growth under direct stimulation.

Experiment 75. *Effect of long-continued indirect stimulation.*—In the case of Mimosa, it was shown that indirect

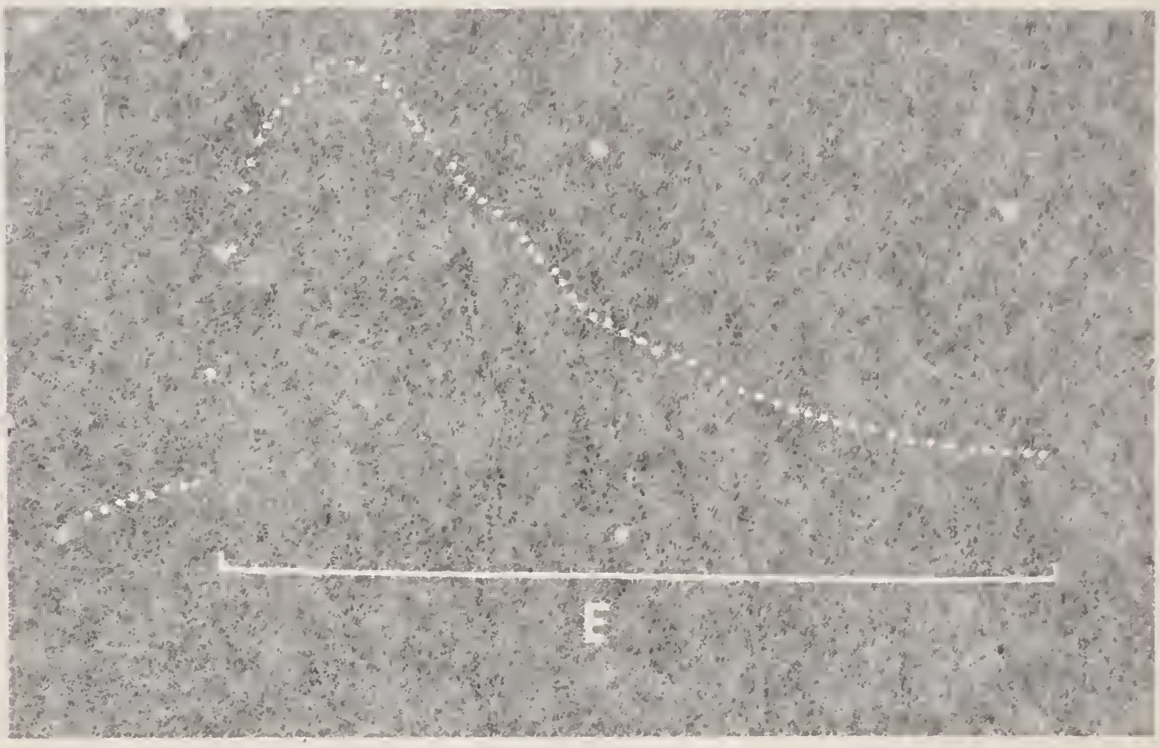


FIG. 70. Effect of continuous indirect electric stimulation E. Preliminary enhancement of growth followed by excitatory contraction. Interval of successive dots 10 seconds. (Cosmos.)

stimulation induced at first a positive response, which was transformed into negative under prolonged action. Parallel results were obtained with Cosmos under continuous electric stimulation; there was a preliminary enhancement of growth shown by the up-curve, followed by excitatory contraction (down-curve) due to the conduction of true excitation (fig. 70).

ELECTRIC RESPONSE TO DIRECT AND INDIRECT STIMULATION

Employing the electric method of investigation, I have obtained with different organs the positive, the diphasic, and the negative electric responses corresponding to the mechanical responses given by both motile and growing organs.

Experiment 76. *Electric Response.*—I took a leaf of *Bryophyllum calycinum*, and made suitable electric connections,

one with the midrib and the other with a distant indifferent point on the lamina. Radio-thermal stimulation

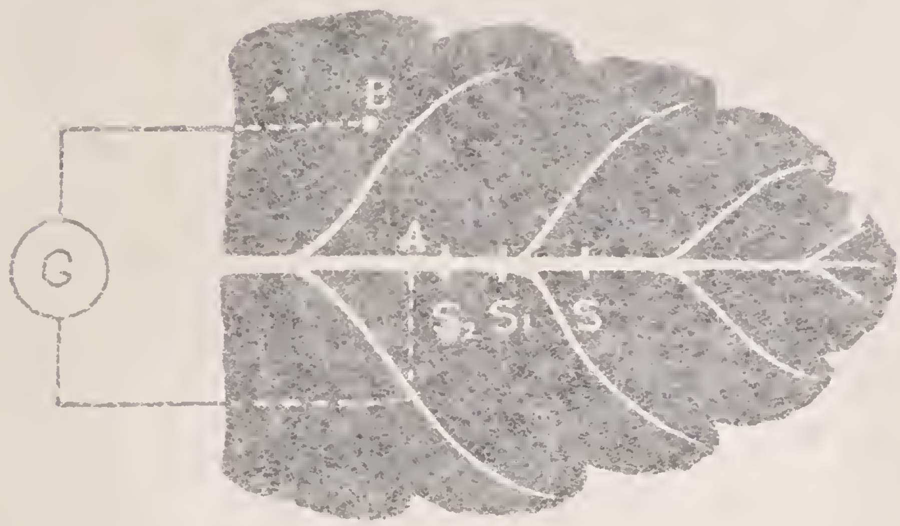


FIG. 71. Diagrammatic representation of electromotive response to indirect stimulation of effectively increasing intensity.

was successively applied, the point of application being gradually brought nearer from S to S_2 (fig. 71). When the

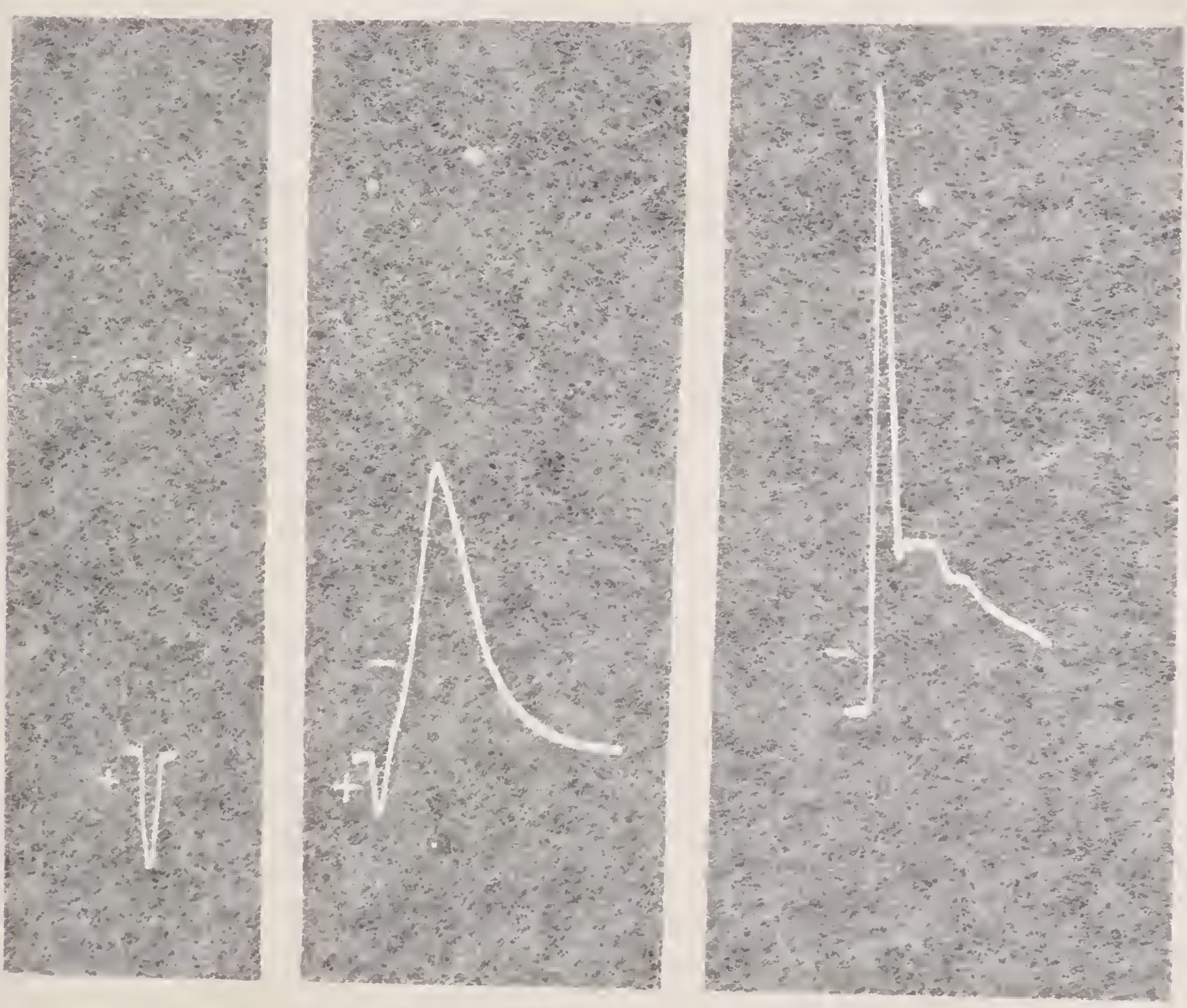


FIG. 72. Positive, diphasic, and negative electric responses (Bryophyllum calycinum).

intervening distance was 20 mm. the response was one of galvanometric positivity. Reduction of the distance to 10 mm. gave rise to a diphasic response, positive followed by negative. When the intervening distance was further reduced to 3 mm. the response was one of galvanometric negativity (fig. 72). This is an independent proof that positive and negative impulses are generated under indirect stimulation.

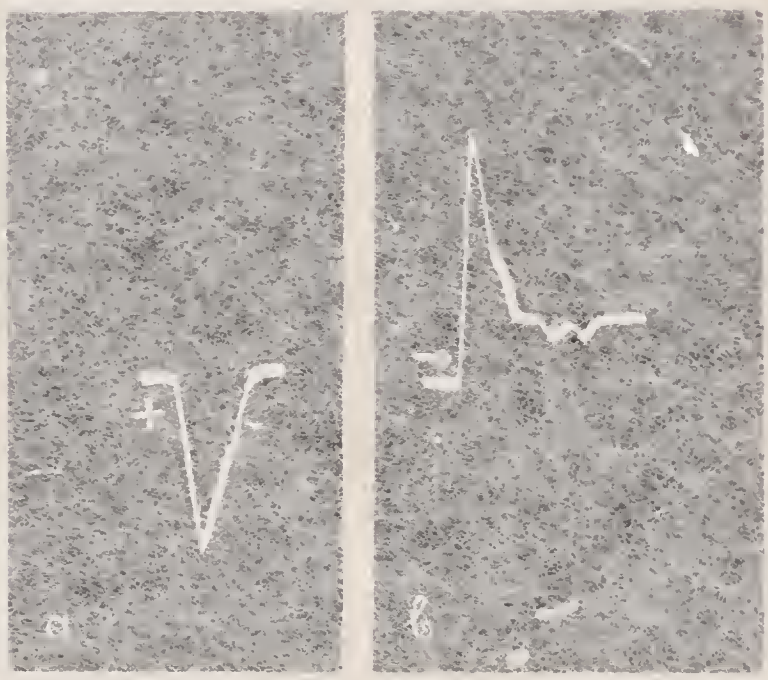


FIG. 73. Electric response at distal and proximal sides under unilateral stimulation.

a, electropositive response at distal, and *b*, electronegative response at proximal side (Helianthus annuus).

Experiment 77. *Electric response at proximal and distal sides under unilateral photic stimulation.*—I took a young flower-stalk of Sunflower (Helianthus) and made suitable electric connections with diametrically opposite sides of the organ for the record of the electric response. On application of strong light on one side of the organ, the electric response at the distal side was *positive*, indicative of expansion and increase of turgor; the electric response at the proximal side was, on the other hand, *negative*, demonstrating contraction and diminution of turgor (fig. 73).

The results obtained by widely different methods of investigation are thus found to be essentially similar; the

different methods employed are the mechanical response of motor organs, the response of growing organs by variation in the rate of growth, and the response by electromotive variation. It has thus been possible to formulate the LAWS OF DIRECT AND INDIRECT STIMULATION :

1. Direct Stimulation .

The effect of moderate intensity of stimulation acting on organs in favourable tonic condition, is contraction, diminution of turgor, negative mechanical and electric response, negative variation (retardation) of the rate of growth.

2. Indirect Stimulation :

(*a*) The effect of feeble stimulation is expansion, increase of turgor, positive mechanical and electric response, positive variation (acceleration) of the rate of growth.

(*b*) The effect of prolonged application of stimulus of moderate intensity is a diphasic response, positive mechanical or electric response followed by the negative ; an acceleration followed by a retardation of growth. If the intervening tissue be highly conducting, the transient positive effect becomes masked by the predominant negative.

These fundamental effects of direct and indirect stimulation are instrumental in bringing about various tropic curvatures. The following table gives the responsive effects induced in pulvini and in growing tissues.

TABLE XV.—SHOWING RESPONSIVE EFFECTS COMMON TO PULVINI AND GROWING ORGANS UNDER UNILATERAL STIMULATION.

Effect of direct stimulation on proximal side	Effect of indirect stimulation on distal side
Diminution of turgor and contraction	Increase of turgor and expansion
Galvanometric negativity	Galvanometric positivity
Contraction and concavity	Expansion and convexity

Positive tropic curvature is brought about by the conjoint expansion of the distal and contraction of the proximal side.

SUMMARY

The response of an organ is modified by the point of application of the stimulus.

The closest parallelism has been established between the response to stimulation given by pulvinated and by growing organs respectively. Conditions which give rise to negative mechanical or electric response also give rise to negative variation or retardation of growth. This is also true of positive mechanical and electric response and positive variation or enhancement of growth.

Effective stimulation is shown to give rise to two distinct impulses: one of these, the positive, is of a hydraulic nature; the negative, on the other hand, is of an excitatory character. The positive is transmitted quickly; the latter, being a phenomenon of conduction of protoplasmic change, is propagated slowly. The positive impulse gives rise to expansion, the excitatory negative to contraction.

Feeble stimulus, especially when acting on a subtonic organ, gives rise only to positive response.

The results of investigation of the effect induced by all forms of stimulation lead to the establishment of the following law: direct stimulation induces contraction; indirect stimulation gives rise to expansion.

Direct stimulation of the responding region causes a contractile fall of the motile leaf, and a retardation of growth in a growing organ. The transmitted or indirect effect of stimulus applied at a distance is to induce an erection of the leaf and an acceleration of the rate of growth.

Tropic movements illustrate the laws of direct and indirect stimulation. The directly excited proximal side undergoes contraction, the opposite distal side undergoes expansion; these two factors conspire to produce a positive curvature.

CHAPTER XIII

DIA-PHOTOTROPISM AND NEGATIVE PHOTOTROPISM

I HAVE explained how under the unilateral action of light the positive curvature attains a maximum. There are, however, cases where under the continued action of strong light the tropic movement undergoes a reversal. Thus to quote Jost: 'Each organ may be found in one of the three different conditions determined by the light intensity, viz. (1) a condition of positive heliotropism, (2) a condition of indifference, (3) a condition of negative heliotropism.'[1] No satisfactory explanation has, however, been found as to why the same organ should exhibit at different times a positive, a neutral, and a negative response. The exhibition of these different effects by an identical organ is incompatible with the theory of specific sensibility, often assumed in explanation of characteristic differences of phototropic response.

Oltmanns found that the seedling of *Lepidium sativum* assumed a dia-phototropic position under intense and long-continued action of light of 600,000 Hefner lamps. He regards this as the indifferent position. But the neutralisation of curvature is, as will be presently explained, not due to a condition of indifference, but to antagonistic effects induced at the two opposite sides of the organ.

PHENOMENON OF NEUTRALISATION

Neutralisation, partial or complete, is principally due to the transverse conduction of excitation across the stem.

[1] Jost, *ibid.* p. 462.

This was demonstrated by the experiment with the stem of Mimosa, in which light was applied on the proximal side, opposite to the indicating motile leaf on the distal side. After the preliminary erectile response, due to indirect stimulation, the leaf exhibited a fall on account of the conduction of the excitatory impulse across the stem (cf. Experiment 76) which induced a diminution of turgor at the distal side. This would antagonise the effect induced at the proximal side by direct stimulation, and neutralise it.

The extent of the neutralisation will therefore depend (1) on the transverse conductivity of the tissue, and (2) on the intensity and duration of the incident stimulation. Other things being equal, neutralisation will be incomplete in a thick, and complete in a thin, stem. The following experiments were undertaken in verification.

Experiment 78. *Partial neutralisation.*—The moderately thick stem of *Dragea volubilis* was exposed to the unilateral action of an arc-light. The first effect was a positive phototropic curvature, which, after reaching a maximum was partially neutralised under continued action of the light for 2 hours.

Experiment 79. *Complete neutralisation.*—The thin stem of a young seedling of Phaseolus does not offer so great a resistance to the transverse conduction of excitation as a thick stem. When light from Pointolite of 30 candle-power was unilaterally applied on the seedling, the maximum positive curvature was induced in about 2 minutes. This curvature was, however, completely neutralised under the continued action of light for 5 minutes.

Strong and prolonged unilateral stimulation does not, however, end in mere neutralisation, which places the organ at right angles to light, regarded as the dia-phototropic position. The transformation is carried still further; thus, three stages of phototropic action may be distinguished: positive at the beginning, neutralisation or dia-phototropic attitude as the intermediate, and negative phototropism as the final effect. How is this final transformation effected?

Fatigue-Relaxation

There is a difficulty in connection with the reversal of positive curvature into negative which cannot be explained simply by the conduction of excitation transversely from the stimulated to the opposite side; for, in a radial organ, the contraction of the distal side cannot be greater than that of the directly excited proximal side. There must therefore be an additional factor in operation, which has to be discovered.

The following experiments prove that it is *fatigue-relaxation* which occurs in a tissue under continued stimulation.

As an example, in illustration of this fact, may be cited the erectile movement of the leaf of Mimosa after continuous stimulation. When the leaf is subjected to brief electric stimulation there is an immediate fall of the leaf, due to active contraction of the more effective lower half of the pulvinus. The leaf then exhibits normal erectile recovery. When the leaf is subjected to continuous stimulation it also exhibits a preliminary fall with subsequent erection of the leaf, this erection being due to fatigue-relaxation of the lower half of the organ.[1] The result is not unlike the contraction of a muscle passing into relaxation under continuous stimulation.

The preliminary phases culminating in fatigue-relaxation in growing organs I propose to demonstrate:

1. Under different *intensities* of stimulation, successively applied to the plant; and
2. Under uniform strong intensity, but increasing *duration* of application.

I will first describe the general effects of brief and of prolonged electric stimulation on growing organs.

Experiment 80. *Normal contraction and recovery after brief electric stimulation.*—I took a specimen of Cow-pea (*Vigna Catjang*) and obtained record of its normal rate of

[1] *The Motor Mechanism of Plants* (1928), p. 56.

growth on a moving plate. The ascending part of the curve (fig. 74) represents the normal rate; direct application of electric stimulus at horizontal arrow (intensity 2 units and duration 2 seconds) induced contraction indicated by the down-curve. Slow recovery occurred till the normal rate of growth was restored. *After this normal recovery, the plant exhibited contraction on fresh stimulation.*

Experiment 81. *Fatigue-relaxation of growth under continued stimulation.*—After the normal recovery the identical specimen was continuously subjected to an electric stimulus of 2 units. The response now was a preliminary down-curve of contraction, succeeded by an up-curve of relaxation (fig. 75). An outward resemblance will be noticed in the two records (figs. 74, 75). The inner difference lies in the fact that *after apparent recovery consequent on fatigue-relaxation, the plant does not exhibit contraction on fresh stimulation, as it does after normal recovery.*

FIG. 74. Effect of electric shock of short duration at arrow induces contraction, followed by normal recovery (Vigna Catjang).

In the experiments described the stimulus employed was electric. I next investigated the effect of intense photic stimulation on a growing plant.

Experiment 82. *Fatigue-relaxation under strong light.*—I took a seedling of Oryza, and strong light was made to act, by means of inclined mirrors, on all sides of the plant. The result obtained at the first stage was normal contraction and retardation of growth, followed later by relaxation under the prolonged stimulation.

From the above facts it is clear that stimulation induces

definite reactions which modify the rate of growth, *i.e.* a contraction under moderate, and relaxation under intense and prolonged, stimulation. Hence tropic curvature brought about by one-sided action of light would likewise be subject to modification, according to the intensity and duration of the incident illumination, by two factors: (1) the transverse conduction of excitation to the distal side, and (2) the fatigue-relaxation at the proximal side. This explanation is based on the following experiments.

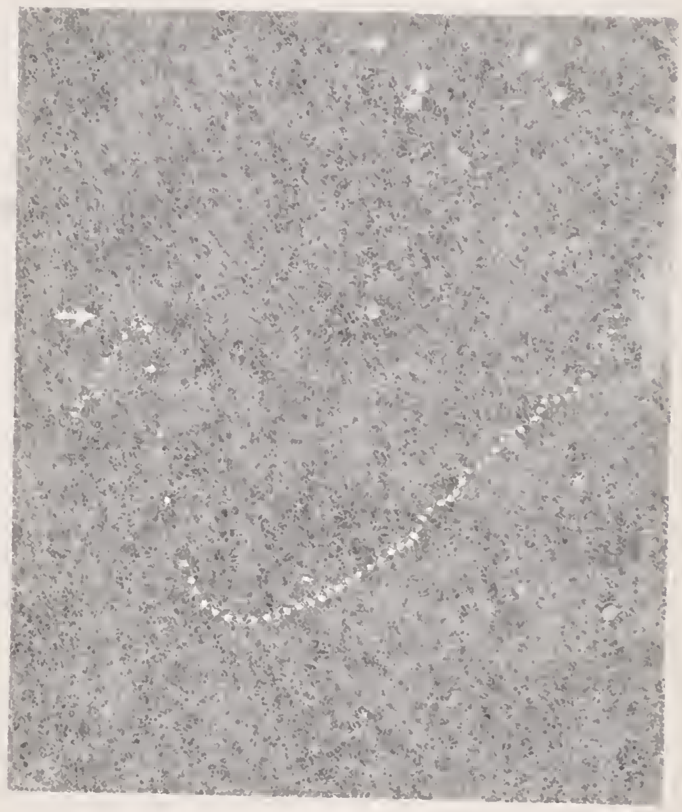


FIG. 75. Effect of continuous electric stimulation at arrow onwards induces contraction followed by fatigue relaxation (Vigna Catjang).

NEGATIVE PHOTOTROPIC CURVATURE

Experiment 83. *Effect of varying intensity of light.* The growing organ was moderately thin; it was subjected to unilateral action of light from a 16 candle-power incandescent lamp placed at a distance of 10 cm. A maximum positive curvature was induced in the course of 50 minutes. The intensity of light was then increased by bringing the lamp nearer, the intervening distance being reduced to 6 cm. After an exposure of 70 minutes to the stronger light the specimen assumed a dia-phototropic position of equilibrium. Sunlight was next applied, and there was a pronounced reversal into negative phototropic curvature in the course of 30 minutes.

Experiment 84. *Phototropic reversal under continued action of strong light.*—The change of response from positive to negative, described in the previous experiment, was brought about by successive increase in the intensity of

light. In the present case very strong light from an arc-lamp was applied from the beginning, and a *continuous*

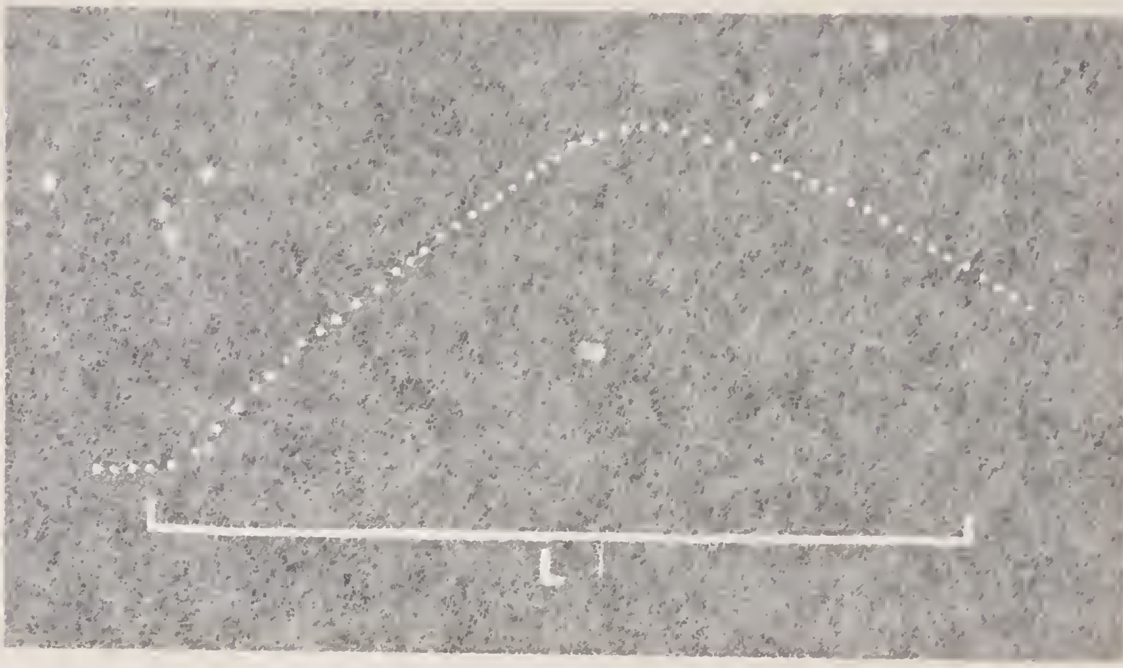


FIG. 76. Phototropic reversal under continued action of strong light L (Vicia Faba).

record taken of the change in the sign of response of the young shoot of *Vicia Faba*. The first effect was a positive curvature which attained its maximum in the course of 5 minutes; after this there was neutralisation, succeeded by negative curvature (fig. 76).

FIG. 77. Positive, dia- and negative phototropic response of Oryza under continued unilateral stimulus of intense light.

Experiment 85. *Transformation of positive into pronounced negative in Oryza.*—Since transverse conduction is more rapid in a thin specimen, I expected to obtain a quicker reversal in Oryza. Light from an arc-lamp produced maximum positive curvature in the course of 2 minutes, after which there was neutralisation. Subsequently complete and pronounced negative phototropic reversal occurred in the course of a further minute and a half (fig. 77).

Supposed Phototropic Ineffectiveness of Sunlight

A brief reference may be made here of the apparently anomalous phenomenon that 'direct sunlight is too bright to bring about heliotropic curvature; only diffuse and not direct sunlight has the power of inducing heliotropic movements.'[1] It is inconceivable that sunlight should have lost all phototropic power because it is so bright. The experiments just described give an adequate explanation of the apparent ineffectiveness of bright light. It has been shown that the tropic curvature, under moderate intensity of light, does not undergo any neutralisation, but that under very high intensity of bright light transverse conduction occurs, which causes the undoing of the curvature. This is demonstrated by the record already given of the continuous action of strong light, showing that the normal positive curvature at the beginning became neutralised later.

Negative Phototropism of Roots

The abolition of geotropic reaction in the root, after amputation of the tip, has led to the conclusion that the tip is the *perceptive organ*, the responding organ being at the growing region at a short distance from the root-tip. On the analogy of the opposite geotropic responses of shoot and root, the hasty generalisation has been made that the sign of response of root to light is opposite to that of the stem, a negative instead of a positive curvature. The conclusion was apparently supported by the negative phototropic curvature of the root of *Sinapis*. The supposed analogy is, however, false; for while in the case of the root the stimulus of gravity acts only on the restricted area of the tip, the stimulus of light is not necessarily so restricted, since it can act not only on the tip, but also on the region of growth. That there is no universal analogy between the action of light and gravitation is seen from the fact that while gravitation induces in the root a movement opposite

[1] Jost, *ibid.* p. 464.

to that in the shoot, light does not always produce this opposite reaction; *for though some roots turn away from light, others move towards it.*

The difficulty encountered in obtaining a direct record of the phototropic curvature of the root was great. It was overcome by the use of a sensitive recorder, and by the employment of roots which possessed a moderate amount of rigidity, so that the induced curvature could exert a sufficient pull on the recording lever. One of the most suitable plants is *Ipomoea reptans*, which floats on ponds, the roots normally growing vertically downwards. The aerial roots of certain plants were also found suitable for the investigation.

The Root-Recorder

The Recorder (fig. 78) consists of a very light writing lever W, the axis carrying an aluminium wheel of a small diameter.

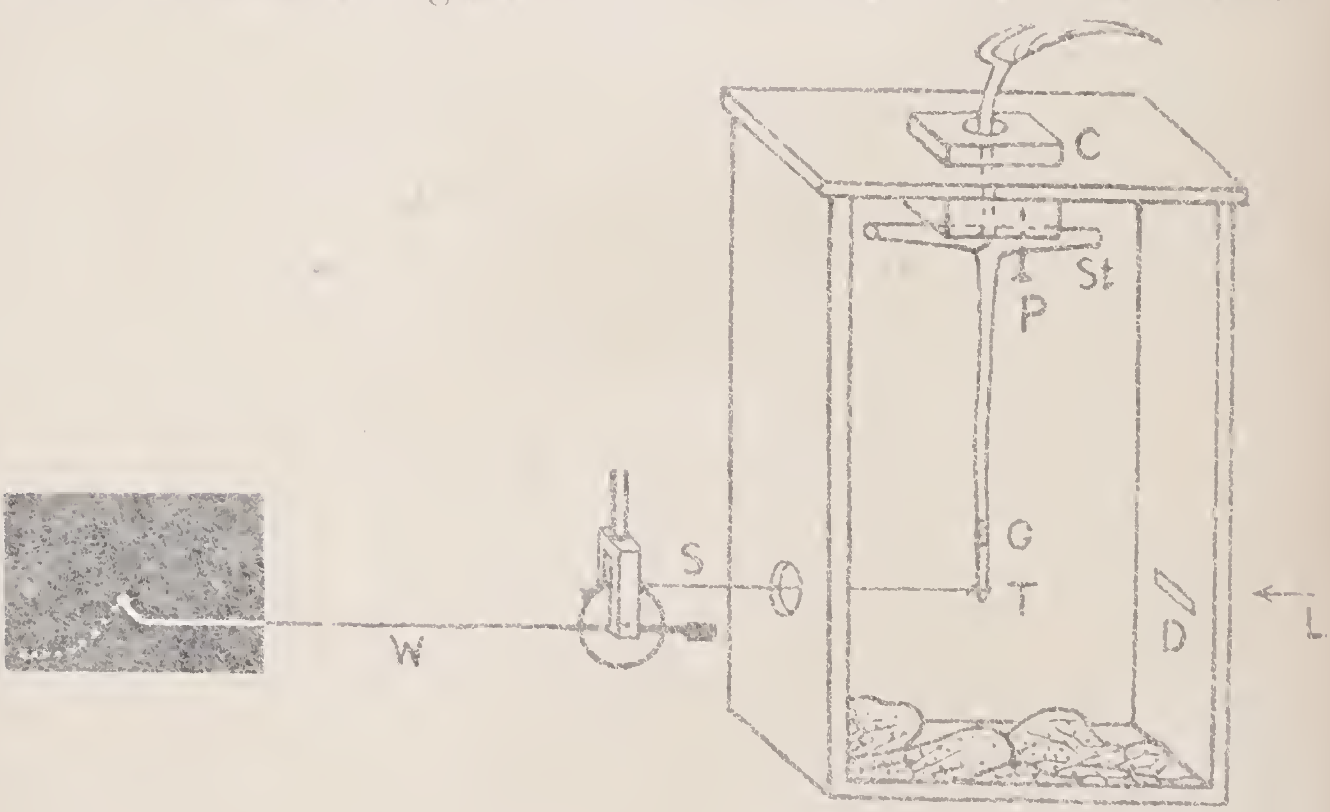


Fig. 78. The Root-Recorder. (*See text.*)

A string S, appropriately attached to the wheel, is tied to the tip of the root T, the growing region G being a little above the tip. The stem St is fixed on a piece of cork by the pin P, the root projecting vertically downwards. The plant is suitably mounted in a rectangular trough of mica,

kept in a proper humid condition by pieces of sponge soaked in water. There are two small openings, one to the right for the passage of light through a narrow horizontal diaphragm D, the other to the left for the passage of the string attached to the recorder. The cork supporting the root can be adjusted up or down, so that either the root-tip or the growing region or both can be exposed to the action of light.

The following experiments were carried out to determine the effect of unilateral photic stimulation (1) on the root-tip, and (2) on the growing region of the root.

Effect of Unilateral Stimulation of the Root-Tip

Experiment 86.—The tip of the root of Ipomoea was subjected to the unilateral action of light for 70 seconds.

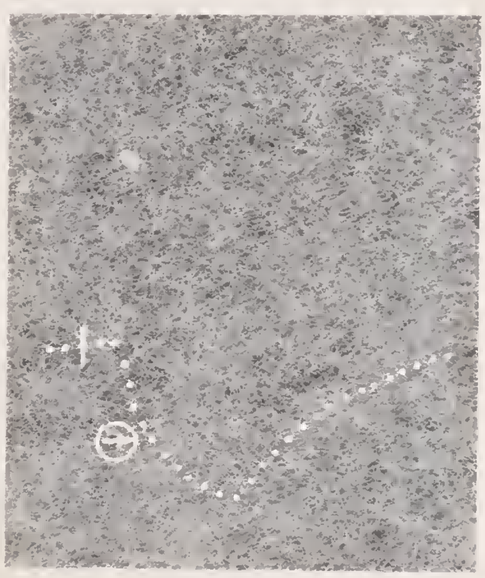


Fig. 79. Negative response of the root to indirect stimulation (Ipomoea).

Vertical line indicates moment of application, and horizontal arrow within circle, of the withdrawal of light.

The source of light was a 100-candle-power Pointolite. The curvature induced was found to be *negative* or away from the source of light, initiated within 15 seconds of the exposure to light. The negative movement continued for 1 minute after the cessation of light, after which there was complete recovery (fig. 79).

Since the responding growing region is at some distance from the tip, the stimulation of the root was indirect in this experiment. The negative curvature of the root in response to indirect stimulation is by no means unique, for a similar effect is induced by indirect stimulation of the shoot, as shown in the following experiment.

Effect of Indirect Unilateral Stimulation of Shoot

Experiment 87.—I took a young shoot of *Vicia Faba*, and after finding its region of maximum growth, applied unilateral light at a distance of 5 cm. below that region, the

Fig. 80. Negative response of shoot under indirect unilateral photic stimulation (Vicia Faba).

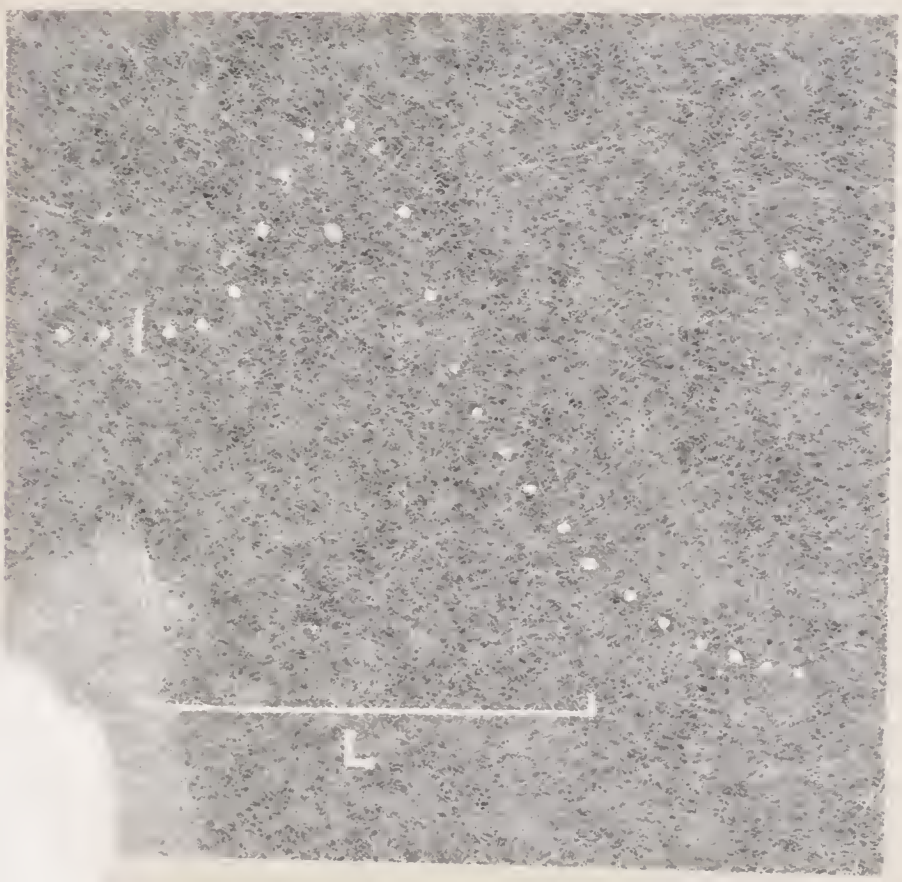
moment of application being indicated by the vertical arrow in the record. The stimulation was, therefore, indirect. Light is seen to have induced *negative* curvature, shown by the down-curve, which persisted for a while after the cessation of light marked by the horizontal arrow within the circle. There was a subsequent recovery which was complete (fig. 80).

I have obtained a similar negative response on the

unilateral stimulation of the tip of the shoot, when the tip happened to be at a certain distance from the region of active growth. The final result is somewhat dependent on the conducting power of the intervening length of tissue. In cases where the tissue is highly conducting, the excitatory negative impulse, reaching the growing region, induces a positive curvature.

Effect of Simultaneous Stimulation of the Tip and of the Growing Region of Root

When the growing region of the root is directly stimulated by unilateral light, the response is a positive curva-



[illegible] Effect of simultaneous unilateral stimulation [illegible] and of the growing region of root (Ipomoea). [illegible] ive dots at intervals of 10 seconds.

[illegible] ast with the negative curvature induced [illegible] stimulation (*cf.* also Experiment 86). I next [illegible] the effect of simultaneous direct and indirect [illegible] stimulation of the root.

Experiment 88.—In a specimen of Ipomoea both the tip and the growing-point were simultaneously stimulated by unilateral light from a 100-candle-power Pointolite. The effect of stimulation of the tip alone would, as already shown, be negative, while that of the growing region would be positive. Since the resultant effect was positive, the response of the growing region, at least in the present case, was relatively the more effective. The positive response occurred 20 seconds after the incidence of light and reached a maxi-

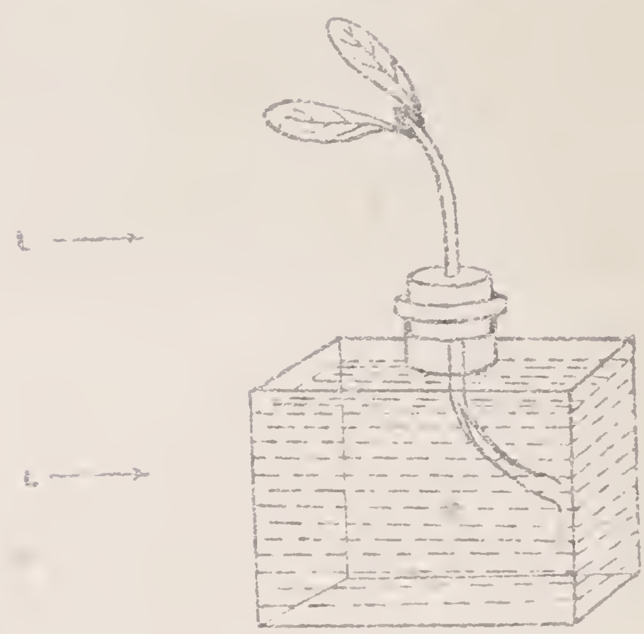


FIG. 82. Effect on shoot and root of unilateral exposure to light (Sanchezia).

mum after 70 seconds. After this there was a reversal of response from positive to negative, due to transverse conduction of excitation across the organ from the [illegible]mal to the distal side (fig. 81). The extent of [illegible]rsal obviously depends (1) on the transverse con[illegible] and thickness of the root, and (2) on the intensity [illegible]tion of the illumination.

Three characteristic types of response of th[illegible] t are met with:

1. Positive curvature;
2. Neutralisation; and
3. Negative curvature.

Referring to the third type, a pronounced ne[illegible] curvature occurs under prolonged unilateral stimulatio[illegible]

the root, especially when it is thin, a condition which facilitates transverse conduction of excitation to the distal side.

Should the power of transverse conduction in the shoot be less than that in the root, then under the action of the same unilateral stimulation by light the stem would exhibit a positive, while the root would show a negative, curvature. This is seen in the illustration (fig. 82), reproduced from a photograph, of the responsive curvature of stem and root of *Sanchezia nobilis*. The stem, being thick, failed to transmit excitation to the distal side; the phototropic curvature was therefore positive. But transverse conduction occurring in the root induced the negative phototropic curvature.

Phototropic Curvature of Root of Sinapis

I next investigated the effect of unilateral light on the thin root of *Sinapis* by taking a continuous record of its movements. The root was too thin to give a direct record by exerting a pull on the recording lever. The experiment was therefore modified as follows:

Experiment 89.—The plant was mounted with its root immersed in a cubical glass vessel. A microscope with micrometer eye-piece was focused on the tip of the root. Light from a 100-candle-power Pointolite was applied laterally on one side, say the left. The incidence of the lateral light at first induced a movement towards the light (positive curvature), which went on increasing for 15 minutes, after which there was a turning away from light. There was neutralisation in the course of about 28 minutes, after which an increasing negative curvature was produced. The following table gives readings of the scale taken every minutes, the positive readings indicating the movement of the root towards, and the negative readings that away from, the light.

TABLE XVI.—EFFECT OF UNILATERAL LIGHT ON THE ROOT OF SINAPIS.

Intervals of time.	Responsive movement, Positive and Negative.
0	0
5 minutes	+ 1·0
10 ,,	+ 1·8
15 ,,	+ 2·1
20 ,,	+ 2·0
25 ,,	+ 1·3
30 ,,	+ 0·5
35 ,,	− 0·3
40 ,,	− 0·9
45 ,,	− 1·4
50 ,,	− 1·8
55 ,,	− 2·1
60 ,,	− 2·4

The curve obtained from the above data (fig. 83) clearly shows how the root at first moves towards the light and

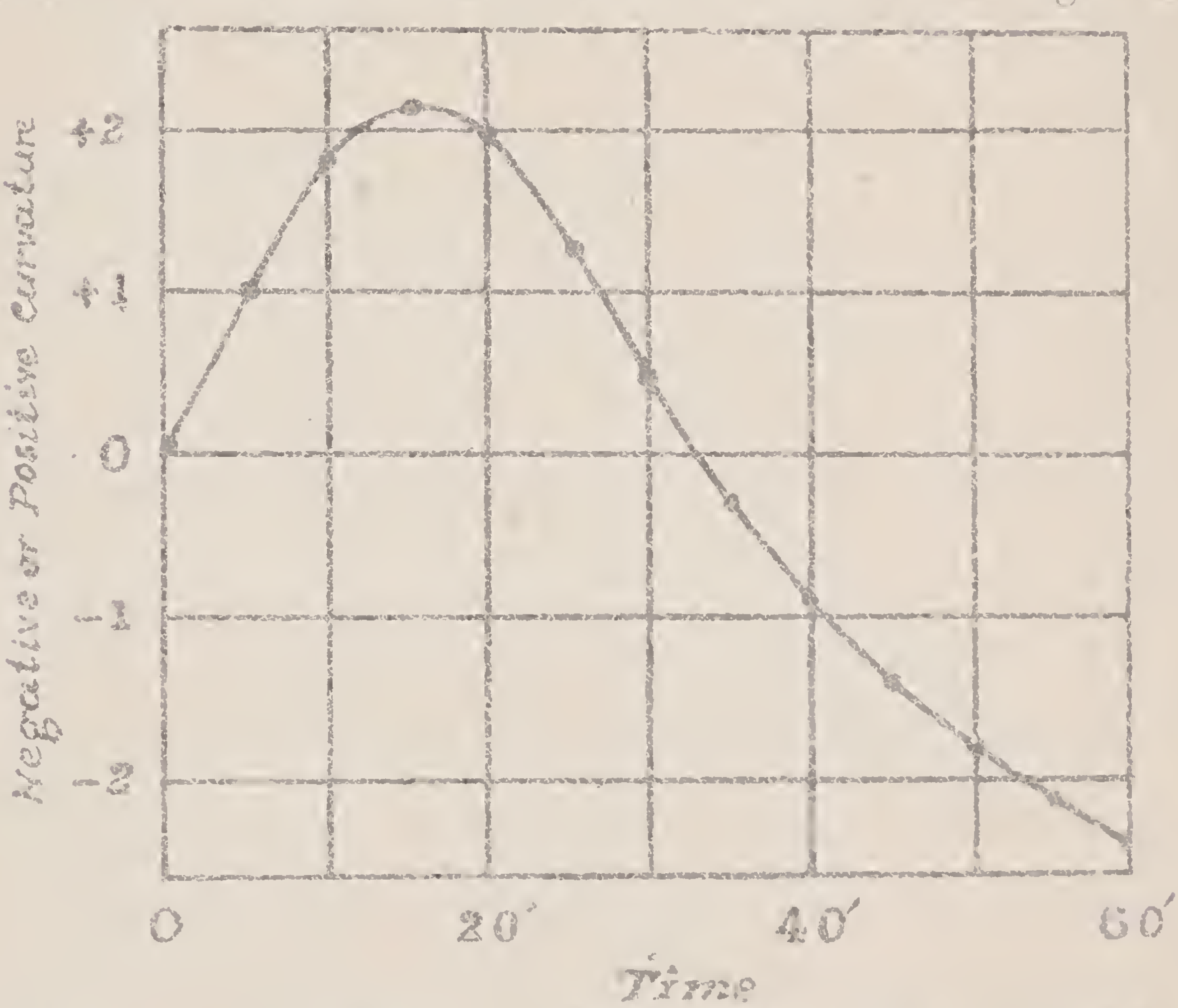


FIG. 83. Response of root of Sinapis under continued unilateral action of light.

The sequence of response is positive, neutralisation, and pronounced negative.

then moves away from it, passing through the stage of neutralisation.

SUMMARY

The normal effect of direct unilateral stimulation by light is a positive curvature.

Transverse conduction of excitation to the distal side induces neutralisation, that is, a dia-phototropic attitude of the organ.

Stronger and long-continued action of light transforms the positive into a negative curvature. An important contributory factor in the reversal of response is the fatigue-relaxation of the proximal side of the organ.

Investigation of the action of light on the root shows that the irritability of the root is in no way different from that of the shoot.

The effect of unilateral illumination of the tip of the root is the indirect stimulation of the growing region by transmitted impulse; this induces acceleration of the rate of growth on the stimulated side which causes negative curvature. The shoot gives a similar response to indirect stimulation.

In a thick root, in which there is no transmission of excitation to the distal side, the response is a positive phototropic curvature.

In a thin root, such as that of Sinapis, the sequence of response is positive, dia-phototropic, and finally negative due to the transmission of excitation across the thin organ.

It was want of knowledge of the preliminary positive curvature of the root that led to the erroneous inference that the root possesses an irritability specifically different from that of the shoot.

CHAPTER XIV

THE PHOTOTROPIC CURVE AND ITS CHARACTERISTIC

The characteristics of the phototropic curve will be stu in greater detail in this chapter, any point in the c exhibiting the relation between the stimulus of light the effect induced by it. The effective intensity of stim tion has been shown to depend on the duration of expo (p. 112). It has been further shown (1) that in the sim cases the reaction under continued unilateral stimulatio light is one of increasing phototropic curvature ; (2) the tropic curvature is modified by the transverse condu of excitation across the organ from the proximal distal side.

I will first consider the contractile reaction induc a growing organ under continued action of diffuse ex stimulation, either electric or photic. The reaction- is obtained by making the plant record, by means o High Magnification Crescograph, the increasing retard of its growth (incipient contraction). Two records the effects of continuous electric and photic stimula have already been given (*cf.* fig. 39), in which the ord of the curve represents the incipient contraction and abscissa the duration of application of the stimulus contraction was seen to be slight at the first stage increased rapidly in the second, after which it declined reached a limit at the third stage. The excitatory traction is thus not constant throughout the whole but undergoes very definite and characteristic vari To facilitate explanation of certain characteristic e

I use the necessary new term *susceptibility* to indicate the relation between the stimulus and the resulting excitatory contraction; this latter will often be designated by the shorter term *excitation*:

$$\text{Susceptibility} = \frac{\text{Excitatory contraction}}{\text{Stimulus}}$$

Different organs of plants exhibit unequal susceptibilities; some undergo excitation under feeble stimulation, while others require more intense stimulation to induce it. Even in one identical organ the susceptibility will be found to undergo a characteristic variation, being feeble at the beginning, considerable in the middle, and becoming feeble once more towards the end.

The Simple Phototropic Curve

The simple phototropic curve is obtained, as already explained, by making the plant-organ record its movement under continuous action of light applied on one side. Curves were obtained in this way, of both pulvinated and growing organs.

Characteristic Curve of Erythrina indica

Experiment 90.—A parallel beam of light from a Nernst lamp was thrown on the upper half of the pulvinus of a leaf of Erythrina, and the increasing positive curve was recorded on a smoked-glass plate which was moved past the writer by a clockwork at a uniform rate. The pulvinus, it should be remembered, does not possess any transverse conductivity. The record (fig. 84) is exactly reproduced from the original by photomechanical process. The successive horizontal dot-intervals of 20 seconds represent equal increments of stimulation during successive equal lengths of exposure. The vertical distances between the dots represent, on the other hand, the corresponding increase

of tropic curvature. The gradient at any point of the curve, the increment of tropic curvature divided by the increment of stimulation, gives the susceptibility for that point. The following table shows how the susceptibility undergoes variation through the whole range of the curve. The

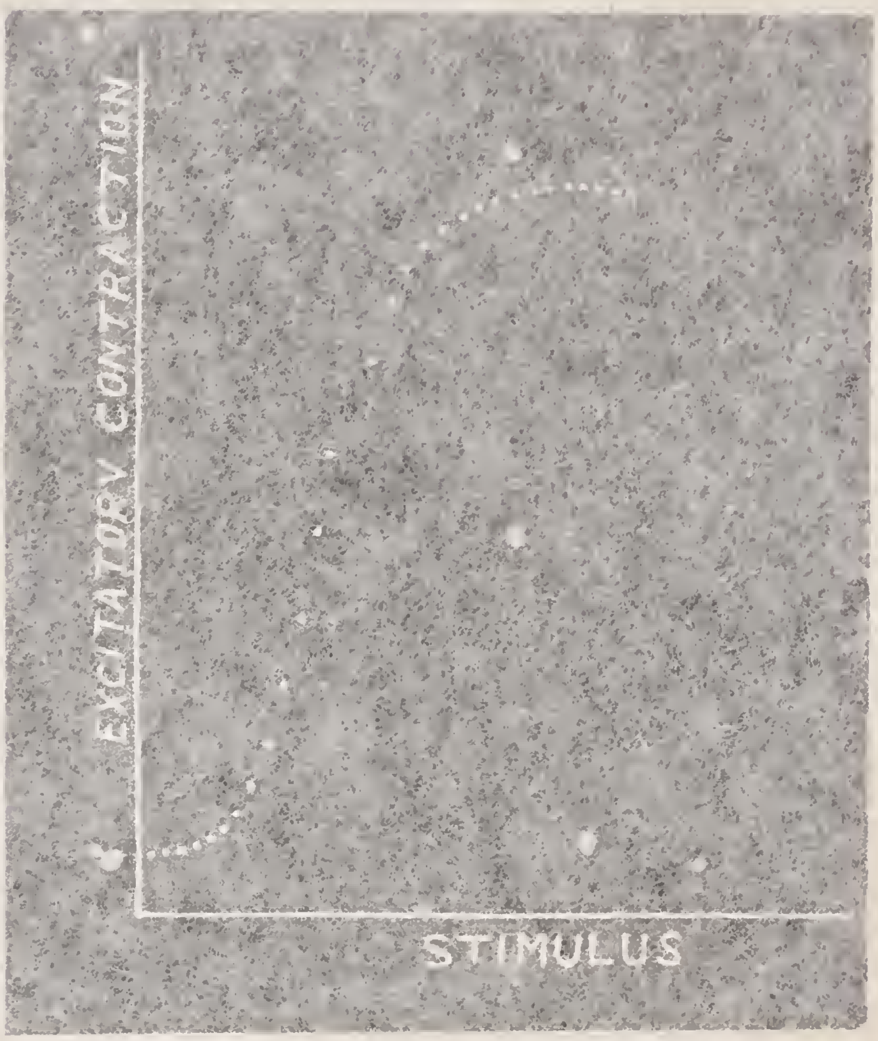


FIG. 84. Simple characteristic curve of phototropic reaction. Excitatory contraction increases slowly in the first part, and rapidly in the second; it is uniform in the third and undergoes decline in the fourth part (Erythrina).

average susceptibility for each point has been calculated from the data furnished by the curve.

The induced contraction which results in tropic curvature is seen to be increased very gradually from the zero point of susceptibility, at which there is no responsive movement. After this, the increase of susceptibility is very rapid, the maximum rate of increase being reached at the point [illegible] of the curve. In the median range the susceptibility is constant, each equal increment of stimulation inducing a

equal amount of tropic curvature. The maximum positive curvature in the present case was attained in the course of 9 minutes. The period of the attainment of this maximum depends on the moto-excitability of the tissue and on the intensity of the incident stimulus. The phototropic curve (*cf.* fig. 86) of growing organs exhibits characteristics similar to those of pulvinated organs.

TABLE XVII.—THE VARIATION OF SUSCEPTIBILITY AT DIFFERENT POINTS OF THE TROPIC CURVE.

Successive points in the curve	Susceptibility for excitatory contraction	Successive points in the curve	Susceptibility for excitatory contraction
1	0	14	6·6
2	0·187	15	4·4
3	0·44	16	2·5
4	0·625	17	1·87
5	0·875	18	1·5
6	1·25	19	1·12
7	1·87	20	0·937
8	3·12	21	0·75
9	5·0	22	0·562
10	6·25	23	0·375
11	8·75	24	0·25
12	8·87	25	0·187
13	8·12	26	0·062

The organ, of which the phototropic curve is given in fig. 84, was in optimum condition; the power of transverse conduction was practically absent. I now take up the more complex case of an organ which was in a slightly subtonic condition at the beginning, and also possessed transverse conductivity.

EFFECT OF STIMULATION OF SUBTONIC ORGAN

It is unfortunate that the terms usually employed in the description of stimulus are so indefinite. A stimulus which is just sufficient to induce excitatory contraction is termed *minimal*, while an intensity below this minimal (*subminimal* stimulus) is tacitly assumed to be ineffective.

The employment of sensitive recorders has, however enabled me to discover the important fact that *subminimal stimulus* is by no means ineffective. It induces a definite reaction of *expansion*, antecedent to the normal *contraction*. A critical intensity demarcates the subminimal from the minimal stimulus, the respective responses being of opposite signs, an expansive positive and a contractile negative.

I have already explained that the critical intensity of stimulus varies in different species of plants. Thus the same intensity of light which induces a retardation of growth (negative variation) in one species may cause an enhancement of the rate (positive variation) in another. The critical point, moreover, depends on the *tonic level* of the organ; in an optimum condition the critical point is low, inasmuch as a feeble stimulus induces the excitatory reaction. In a subtonic tissue, on the other hand, the critical point is high, necessitating a relatively strong and long-continued stimulation to induce the normal reaction. Stimulation itself is found to raise the tonic level of the tissue, so that the response is transformed from expansion to normal contraction.

The physico-chemical processes underlying these opposite responses have, for convenience, been distinguished as the 'A' and 'D' changes. The expansive assimilatory 'building-up' process A is associated with an increase of potential energy of the system. The contractile dissimilatory 'break-down' D is, on the other hand, concomitant with an evolution or run-down of energy.[1]

Returning to the consideration of the action of unilateral stimulation by light in inducing phototropic curvature of an organ in a slightly subtonic condition, the directly stimulated side exhibits expansion at the first stage, causing a negative curvature away from light. But by the continuous action of stimulus the subminimal becomes minimal and then maximal. The negative will thus be transformed

[1] *The Motor Mechanism of Plants* (1928), p. 56.

into normal positive curvature towards the light, which will reach a maximum value.

The organ has been assumed to possess the capacity for transverse conduction. After the attainment of maximum positive curvature, the conduction of excitation across the organ from the proximal to the distal side will bring about a complete neutralisation, to be succeeded by an actual reversal into negative curvature. These theoretical considerations will now be subjected to experimental tests.

The reversal of positive into negative phototropic curvature under strong unilateral illumination usually takes place under an exposure so prolonged that it is difficult to represent the different transformations in a single curve that can be reproduced on a page. This can only be done with a thin specimen, so that the transverse conduction of excitation which induces reversal may take place within a reasonable time. A complete phototropic curve was thus obtained in an identical specimen, which exhibited all the characteristic transformations. For a pulvinated organ, I employed the thin pulvinus of the terminal leaflet of *Desmodium gyrans*. For growing organs, young seedlings of *Zea Mays* were found suitable. In both the above cases the specimens were in a slightly subtonic condition.

Complete Phototropic Curve of a Pulvinated Organ

Experiment 91.—A continuous record was taken (fig. 85) of the action of light from a 50-candle-power incandescent electric lamp incident on the upper half of the pulvinus of the terminal leaflet of Desmodium. This gave rise first to the abnormal negative curvature induced by subminimal stimulation. The curve then proceeded upwards in the direction of positivity, at first slowly, then rapidly. The maximal positive curvature was attained in the course of

18 minutes and remained constant for a short time, as seen in the more or less horizontal record at the top of the curve. After this, transverse conduction of excitation from the

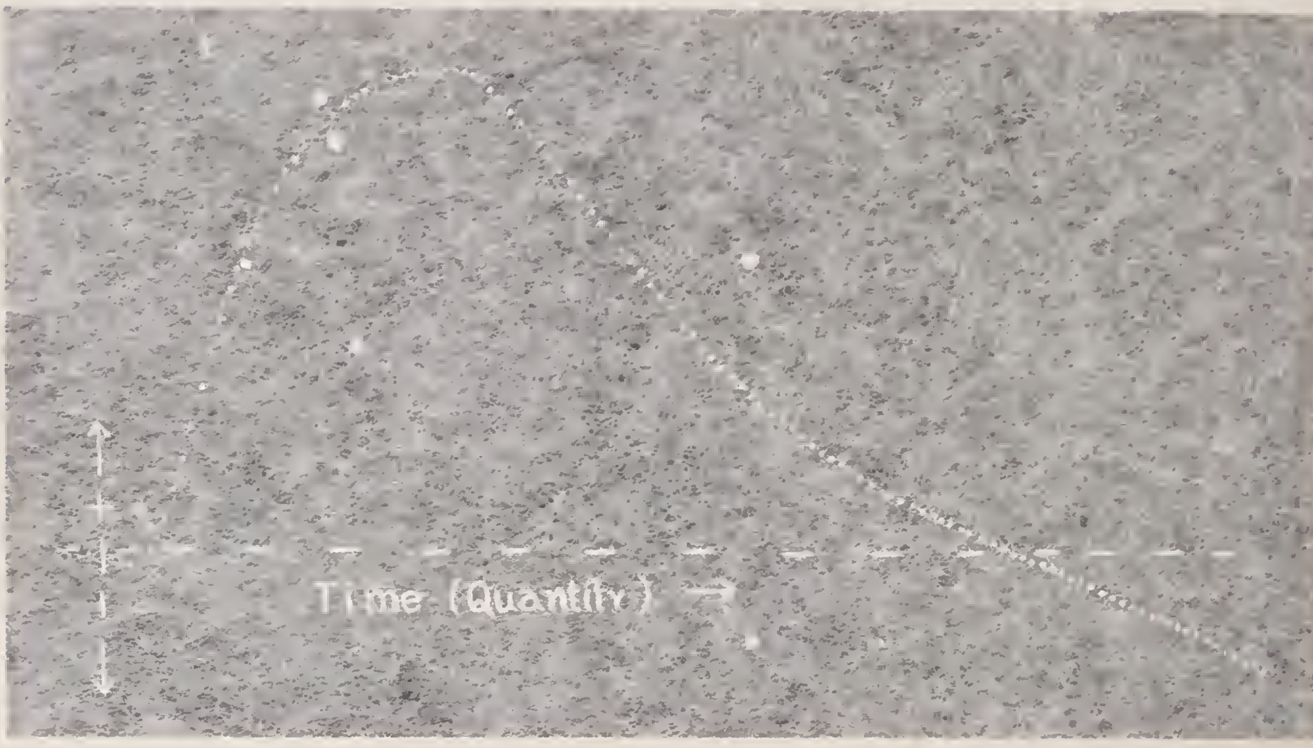


FIG. 85. Complete phototropic curve of a pulvinated organ. Positive curvature above, and negative curvature below, the horizontal zero line. Preliminary negative phase of response due to subminimal stimulus. The positive increases, attains a maximum, and undergoes a reversal. Successive dots at intervals of 30 seconds. Abscissa represents duration of exposure and quantity of incident light. (Terminal leaflet of Desmodium gyrans.)

proximal to the distal side began to take place, inducing neutralisation which was completed in the course of 24 minutes. Subsequently to this, there was a reversal of phototropic curvature into a pronounced negative.

COMPLETE PHOTOTROPIC CURVE OF A GROWING ORGAN

Experiment 92.—A seedling of *Zea Mays* was subjected continuously to unilateral light from a small arc lamp for 2 hours. The characteristics of this curve are very similar to those of Desmodium. The subminimal stimulation induced, at the first stage, a negative curvature; this was transformed into positive after an exposure of

10 minutes, and neutralisation was completed after a further exposure of 43 minutes. The subsequent response became completely transformed into negative (fig. 86).

In the complete phototropic curve of pulvinated and of growing organs, four distinct stages may be distinguished:

1. The stage of subminimal stimulation giving abnormal negative curvature;
2. The stage of increasing positive curvature which reaches a maximum;
3. The stage of neutralisation, and
4. The stage of complete reversal into pronounced negative curvature.

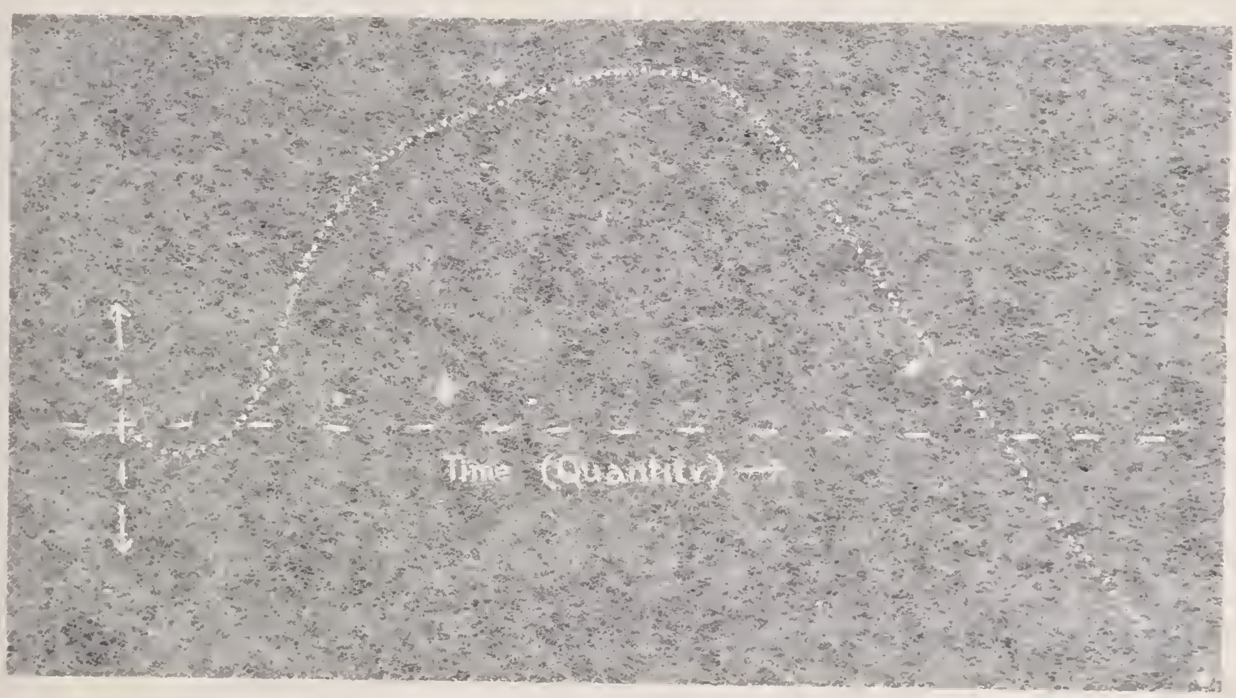


FIG. 86. Complete phototropic curve of a growing organ (Zea Mays).

The phototropic curve crosses the zero line of the abscissa twice; the first crossing takes place *upwards* at the critical point of stimulation which demarcates the subminimal from the minimal. The second crossing *downwards* occurs beyond the point of complete neutralisation.

Neglecting the preliminary negative due to the action of subminimal stimulus, the tropic curve under photic stimulation obeys what is known as Weber's Law. But this is applicable only for a limited range of stimulation; it fails

in the region of subminimal stimulation, where the physio-logical reaction is *qualitatively* different, being expansion instead of contraction.

SUMMARY

A simple phototropic curve exhibits, in the first part, a slow ascent; in the second part the gradient is steep, indicative of a rapid increase of positive curvature; in the third part the rate of increase is uniform; and in the last part the curve tends to become horizontal, indicative of maximal positive curvature.

The susceptibility to stimulation is not the same, but varies in different points of the curve. It is feeble at the beginning, it increases rapidly at the second stage, and reaches uniformity at the median range. Further on, the susceptibility undergoes a rapid decline.

Complicating factors are introduced by a subtonic condition of the tissue, and by the conduction of excitation across the organ from the proximal to the distal side. The complete phototropic curve exhibits, in such circumstances, a negative curvature in the first part, due to physiological expansion under subminimal stimulation. The curve then crosses the abscissa *upwards*, after which the curvature attains its positive maximum. Subsequent to this is the stage of neutralisation brought about by fatigue of the directly stimulated proximal side, and by percolation of excitation across the organ to the distal side. Further stimulation causes the curve to cross the zero line in the *downward* direction, the phototropic curvature being reversed into negative.

CHAPTER XV

THE PHOTONASTIC PHENOMENA

Phototropic response, positive or negative, has been shown to be determined by the directive action of light. There is, however, a different class of phenomena already referred to in previous chapters which is supposed to be independent of the directive action of incident stimulus. This is the so-called photonastic action of light. Strong sunlight, for example, brings about a para-phototropic movement, by which the apices of leaves or leaflets turn towards or away from the strong source of light. The upward movement of the leaflet of Erythrina has already been described. Far more anomalous are the movements of the leaflets of *Averrhoa Carambola* and of *Mimosa pudica*. In Averrhoa the effect of strong light from above is a movement downwards, away from light. In Mimosa the movement under similar circumstances is precisely the opposite.

The above description relates to the action of light from above. What happens when the light acts from below? The results are apparently even more inexplicable, as would appear from the detailed accounts given below.

Response of the leaflet of Averrhoa.—Strong light acting in a downward direction from above induces, as already stated, a movement downwards, away from light. Speaking from the phototropic point of view, this may be described as *negative* phototropism. But when strong light is incident on the leaflet in an upward direction from below the response is also a down-movement towards the light, and [illegible] therefore to be described as *positive* phototropism. This [illegible] the paradoxical conclusion that an identical organ [illegible] two different irritabilities, negative and positive.

Response of the leaflet of Mimosa.—Equally anomalous appears to be the response of the Mimosa leaflet. Strong light acting from above induces a *positive* phototropic movement upwards. But when the direction of the incident light is changed so as to act from below, the responsive movement is still upwards, that is to say, a *negative* phototropic movement away from light.

Such paradoxical reactions led to the employment of the term *photonasty* to describe this class of phenomena, supposed to be totally unrelated to normal phototropic action and due to a different kind of irritability and a different mode of response. Is there really a hiatus between phototropic and photonastic reactions, or is there a possibility of discovering continuity between them? Investigations on the effect of light on the main pulvinus of Mimosa, acting alternately from above and below, gave a valuable clue to the solution of the problem.

It is necessary in this connection to bear in mind the anatomical and physiological characteristics of the two halves of the pulvinus, the upper and the lower. The pulvinus may summarily be described as consisting mainly of two masses of cortex, separated by a thin flexible vascular strand. The relative moto-excitabilities of the two halves of such an anisotropic dorsiventral organ are easily demonstrated by the application of diffuse stimulation, which causes an impulsive fall of the leaf, proving the predominant excitability of the lower half. The excitability of the upper half of the pulvinus is, however, not altogether absent, but relatively feeble, as will be presently demonstrated by local application of stimulus on that half of the organ.

I now describe the characteristic effects of local application of:

1. Feeble stimulus on the upper half;
2. Strong stimulus on the upper half;
3. Feeble stimulus on the lower half; and
4. Strong stimulus on the lower half.

My investigations relate to the effects not only of photic but also of other modes of stimulation, the results being essentially similar in all cases. I shall first deal with the effect of photic stimulation, for which special means have to be devised for the local application of stimulus of feeble and of strong intensity.

LOCAL APPLICATION OF PHOTIC STIMULUS

Feeble or moderate stimulation.—This is secured by a device consisting of an incandescent 4 5 volt pea-lamp placed at one end of a tube, the other end of which is provided with a focusing lens L. The incandescent filament is adjusted horizontally, so that a sharp line of light can be

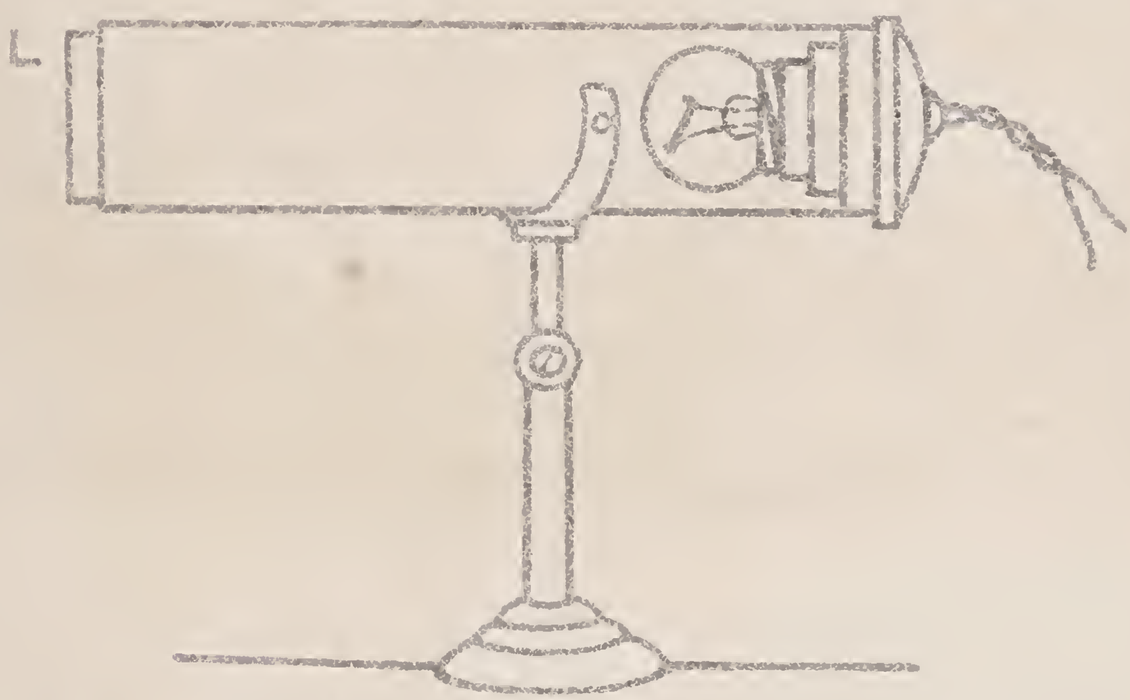


FIG. 87. The incandescent electric lamp-holder. A line of light can be directed vertically downwards on to the upper half, or vertically upwards on to the lower half, of the pulvinus.

thrown across the middle of either the upper or lower half of the pulvinus. The lamp-holder can be raised or lowered; it can be inclined vertically downwards or upwards for the specific purpose of the experiment (fig. 87).

Strong stimulation.—The source of light is a self-feeding small arc-lamp which maintains approximately constant light. The focusing lens gives a horizontal and slightly convergent beam of light; this is thrown vertically either

downwards or upwards by a totally reflecting prism (fig. 88). The two devices just described ensure accurate

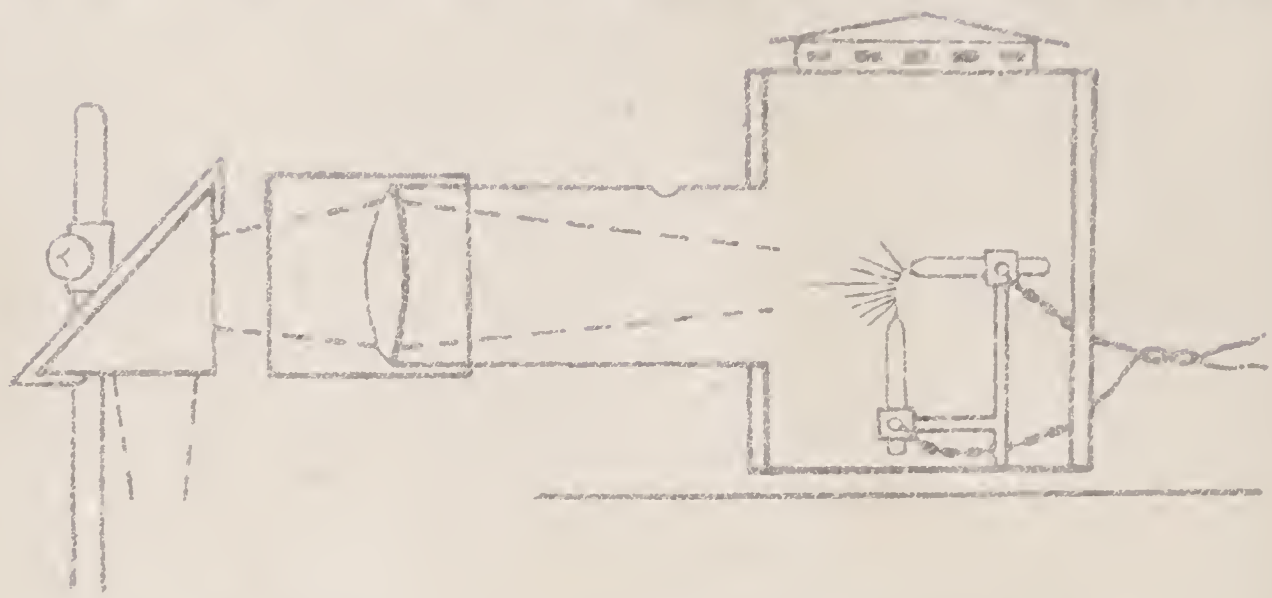


FIG. 88. Arc lamp with totally reflecting prism for application of strong light vertically downwards or upwards.

investigation of the effects of local application of feeble or strong light on the upper and lower halves of the organ.

EFFECT OF LIGHT ON UPPER HALF OF THE PULVINUS

Experiment 93. *Effect of feeble or moderate intensity of light.*—The record, with moderate magnification, was

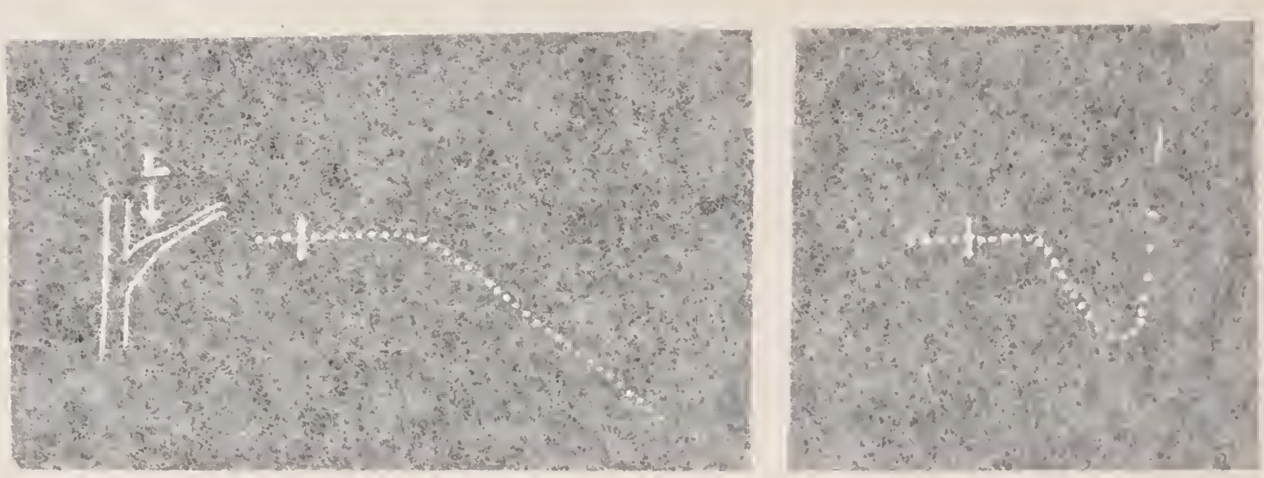


FIG. 89. Records of effect of feeble light (left illustration) and of strong light (illustration to right) on upper half of pulvinus (Mimosa). Successive dots at intervals of [illegible] second. In this and in the following records up-movement is represented by down curve and vice versa.

taken on a fast-moving plate, the successive dots being at intervals of a second. The record to the left (fig. 89)

shows that the responsive movement was upwards towards the light, and that this was initiated after a latent period of 6 seconds. The positive curvature was continuously increased during the whole period of illumination, lasting for 55 seconds or even longer. *Hence moderate unilateral photic stimulation of the less excitable upper half of a dorsi-ventral organ gives rise only to a positive phototropic curvature* The effect of stronger light is, however, strikingly different.

Experiment 94. *Effect of stronger light.*—Stronger light from the arc-lamp induced at first an up-movement towards the light after a latent period of 5 seconds. The positive curvature increased continuously for 10 seconds, after which a very striking change occurred. The erectile movement, due to contraction of the upper half of the pulvinus, became reversed into a down-movement, evidently by the arrival of the excitatory impulse across the boundary line between the upper and lower halves of the organ. The *slow* fall of the leaf at the beginning was due to the successive contraction of the cortical tissue of the lower half of the organ; a short while after this the contractile fall of the leaf became very abrupt, the rapidity of fall becoming so great that a scratch, and not a dot, was produced as the writer was jerked off the plate (right record, fig. 89).

Moderate stimulation of the upper half of the pulvinus is thus seen to give rise to a positive curvature towards the light, while stronger stimulation gives rise to a positive followed by a negative. What can be the reason for this behaviour? The probable explanation is, that under moderate stimulation the downward percolation of excitation along the vertical layers of cortical cells is a slow process on account of the resistance offered by the semi-conducting tissue. But under stronger stimulation the partial block becomes forced, and the excitation not only percolates through the upper half of the pulvinus but also reaches the lower half. The moment of arrival of excitation at the upper boundary of the lower half of the organ is, as already stated, signalled by the inversion of the curve.

The velocity of transmission of excitation through the upper half of the pulvinus can be found from the data given by the record. The thickness of the pulvinus was 2 mm., that of the upper half was 1 mm. approximately. The time of vertical transmission can be found from the record, being the interval between the application of stimulus and the moment of reversal from up to down movement of the leaf. In the present case it was found to be 18 seconds. From this the rate of transmission across the upper half of the organ can be ascertained:

$$\text{Velocity of transmission} = \frac{1}{18} = 0\cdot05 \text{ mm. per second}$$

This velocity I find to vary from 0·01 to 0·1 mm. per second, for the following reasons:

The velocity is increased (*a*) when the thickness of the pulvinus is small; (*b*) when the temperature is near the optimum; (*c*) when the season is favourable; (*d*) when the tissue is in a favourable tonic condition; and (*e*) when the stimulus is strong. The velocity is decreased under opposite conditions.

Effect of Light on the Lower Half of the Pulvinus

Experiment 95. *Effect of moderate light.*—After a latent period of 7 seconds the leaf began to fall downwards

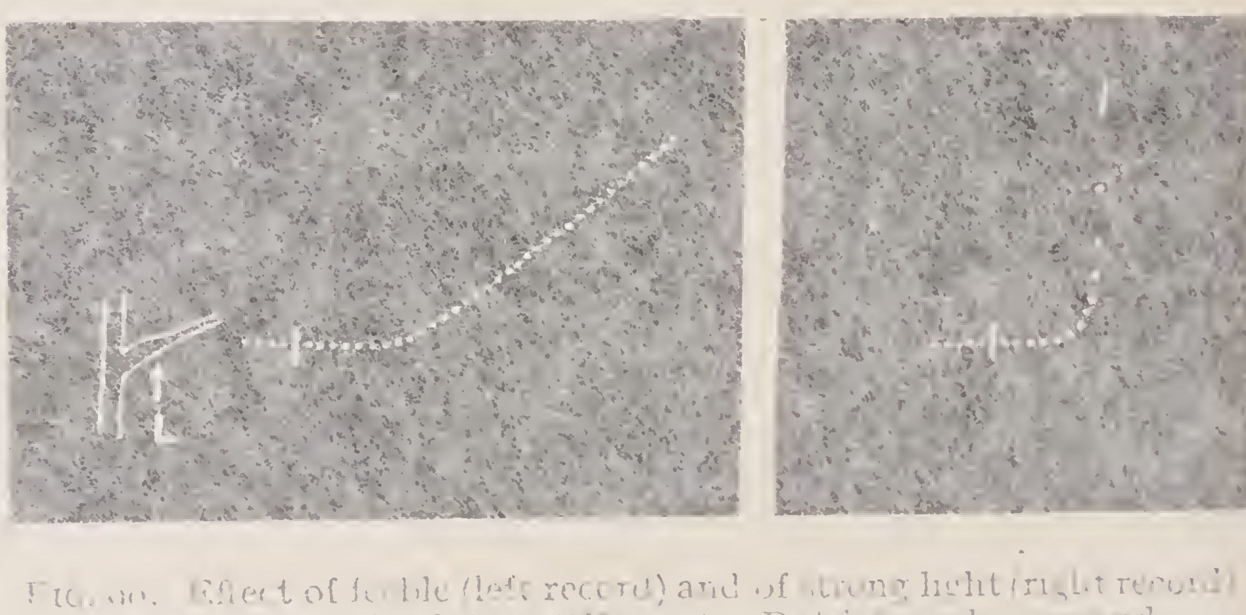


FIG. 90. Effect of feeble (left record) and of strong light (right record) on lower half of pulvinus (Mimosa). Dot intervals 1 second.

towards the light (positive curvature). This slow down-movement continued for 40 seconds or more (left record, fig. 90).

Experiment 96. *Effect of strong light.*—The leaf responded by a fall, that is, positive curvature, after a latent period of 4 seconds. This fall was slow for about 7 seconds, after which it became very abrupt (right record, fig. 90).

I would here draw special attention to the following statement of results regarding the effect of strong light applied on the upper and lower halves of the pulvinus:

1. *Strong light applied above induces a preliminary and short-lived up-response, detectable only by a sensitive method of record. This up-response is followed by a pronounced down-response, that is, with the fall of the leaf.*
2. *Strong light applied below induces a fall of the leaf and a down-response from the beginning, without any other change.*
3. *The effect apparently is the same, whether light be applied above or below, the direction of the responsive movement being finally determined by the contraction of the more excitable half of the organ.*

Physiological Detection of Gradation of Excitability of Different Layers

Some of the characteristics of the response led to the important discovery of a gradation of excitability in the different layers of tissue in the lower half of the pulvinus. An inspection of the curve of response of strong light applied on the lower half will make this clear (*cf.* right record, fig. 90). The responsive fall of the leaf, due to percolation of excitation upwards from layer to layer, was at first slow. It became very abrupt as soon as the excitation reached a certain tissue of the cortex intermediate between the lowermost and uppermost layers in the lower

half of the pulvinus. The same characteristic is observed when strong light acts from above. The arrival of the excitatory impulse at the uppermost layer of the lower half induces a reversal of response from up to down movement. This excitatory fall is, however, slow at the beginning, becoming very rapid as soon as the excitation reaches the highly excitable layers lower down (*cf.* fig. 89). The two results confirm the conclusion that the position of the most excitable tissue is somewhere in the middle of the lower half of the pulvinus. The results of experiments on which this conclusion is based are by no means accidental, but were obtained under all modes of stimulation applied on the upper and lower halves of the organ.

To facilitate explanation, I give a diagrammatic representation of the longitudinal section of the pulvinus, in which the number of layers has been reduced. The vascular bundle F divides the upper from the lower half of the organ. The upper cortex extends from *a* to F; *b* to *d* represents the extent of the lower cortex; *c* represents the hypothetical intermediate layers, the moto-excitability of which is exceptionally high (fig. 91).

Speaking generally, one half of the pulvinus, commonly the lower half, is more excitable than the other; it is this more excitable half that has a determining influence on the movement of response. The positive impulse due to indirect stimulation causes an enhancement of turgor and expansion of this half, giving rise to a positive erectile movement. The excitatory impulse reaching it later causes contraction and fall of the leaf.

Now, if there is a gradation of excitability in the lower half, then the most excitable as well as the most contractile layer *c* will function as *the* essential responding layer. The existence of a specially excitable layer in the lower half of the pulvinus is indicated by the foregoing experiments; for percolation of excitation, either from above or below, to such a layer would account for the abrupt change from a slow to an abrupt fall.

When the stimulus was applied from above or from below the pulvinus, careful observation of the recording lever showed a curious erectile twitch preceding the normal

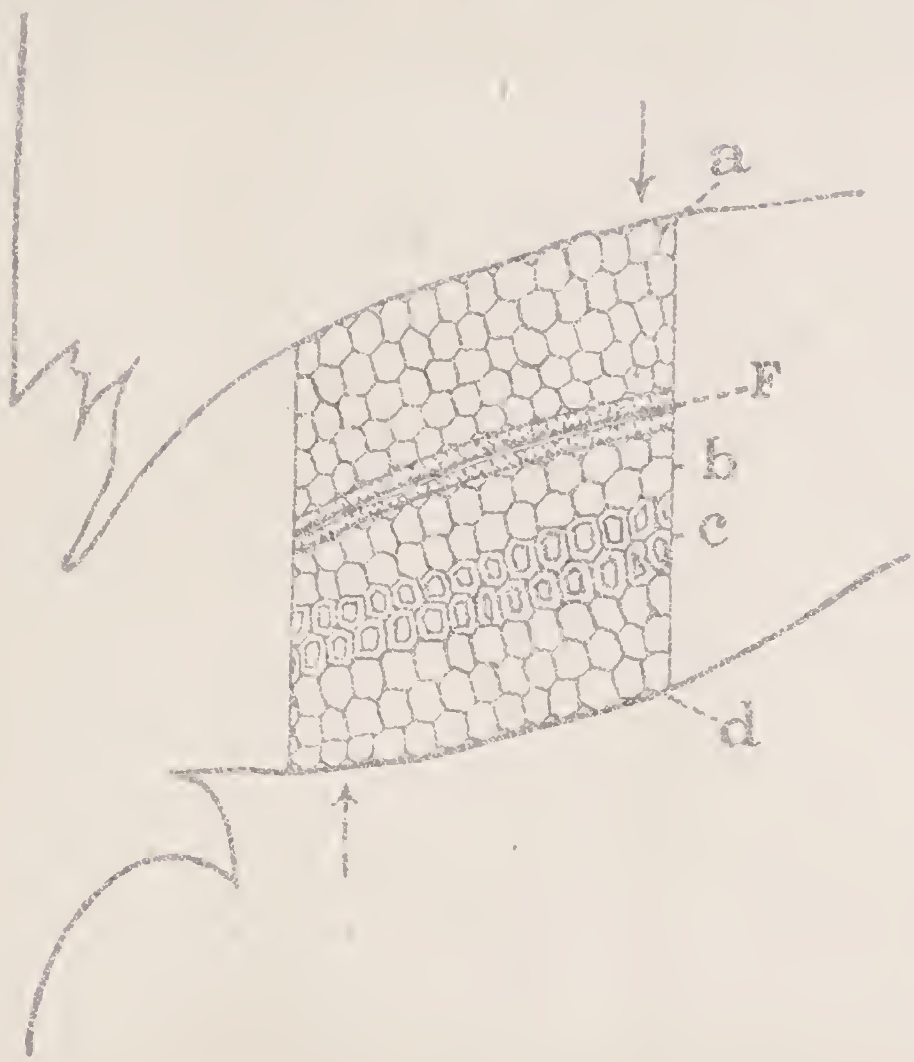


Fig. 61. Diagrammatic representation of the different layers in a longitudinal section of pulvinus

Cortex of upper half extends from *a* to vascular bundle (F); *b*, uppermost layer of lower half; *c*, hypothetical most sensitive layer; *d*, lowest layer of cortex of lower half. Vertical continuous arrow represents application of light on upper, dotted arrow on lower, side

response. This was especially the case when the tonic condition of the specimen was not exceptionally high, so that the rate of percolation of excitation was relatively slow. A satisfactory record of the preliminary twitch, due to positive impulse, was obtained by the employment of a higher magnification.

TRIPHASIC RESPONSE

Experiment 97. *Effect of application of strong light on upper half of pulvinus.*—The record given in fig. 92 gives

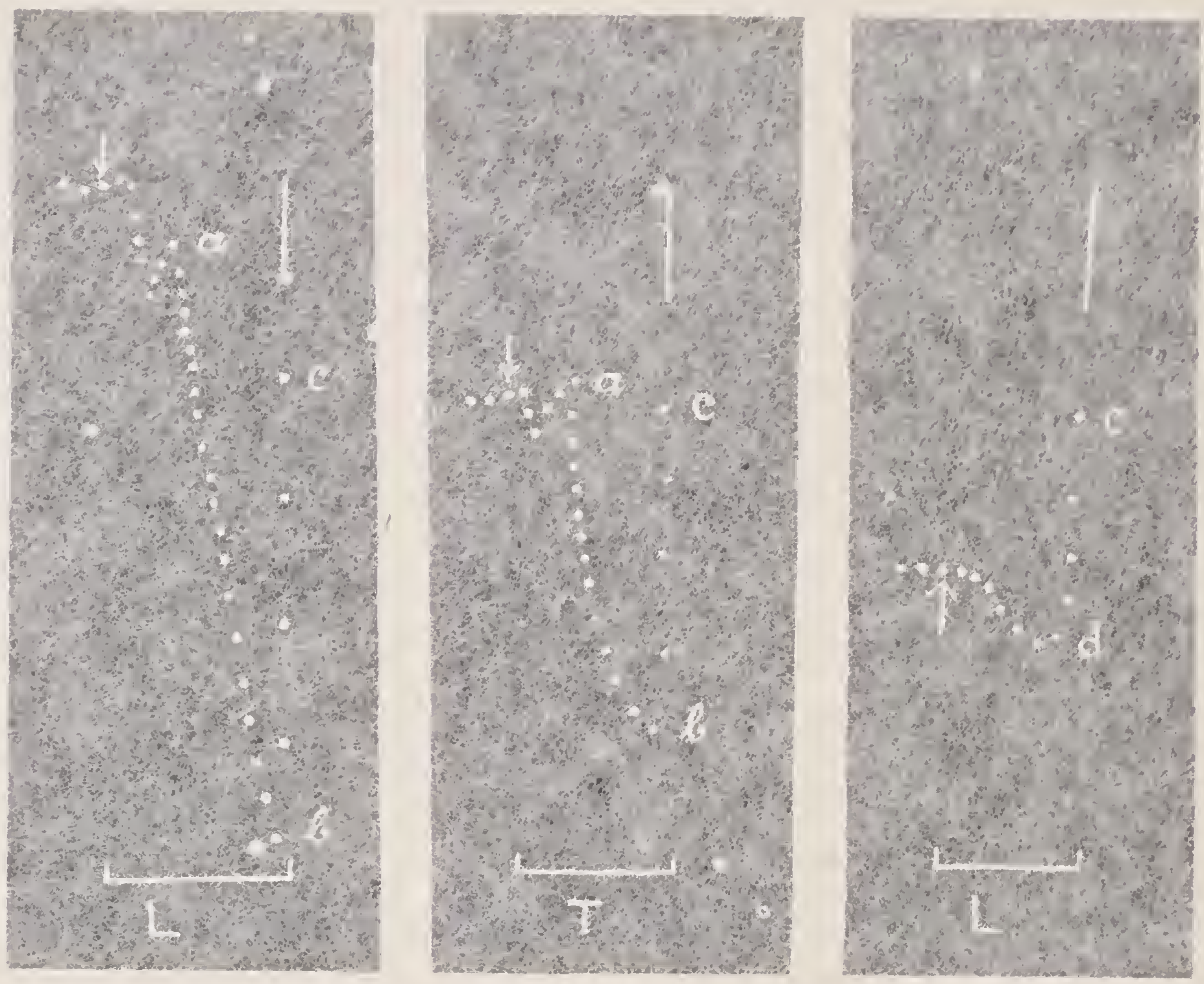


FIG. 92. FIG. 93. FIG. 94.

FIG. 92. Triphasic response on application of light L above (Mimosa).

Preliminary erectile twitch followed by erectile response ($a - b$) due to contraction of upper cortex. Reversal of response to negative fall, slow from b to c and rapid beyond c. (*See* text.)

FIG. 93. Parallel effect of radio-thermal stimulation T applied above.

FIG. 94. Effect of application of strong light L on lower half of pulvinus.

Erectile movements represented by down-curve and *vice versa*.

a striking illustration of the triphasic response. There was at first a short-lived erectile twitch, evidently due to the quick transmission of positive hydraulic impulse which, reaching the most excitable region c, induced expansion and erection of the leaf. This impulse was quickly exhausted.

as evidenced by partial recovery; the contractile response of the upper half of the pulvinus next induced an erectile movement from *a* to *b*. The excitatory impulse then reached the uppermost layer of the lower half of pulvinus and induced reversal of response, which was slow at the beginning from *b* to *c*. But when the impulse reached the most excitable layer *c*, there was an abrupt movement of fall indicated by the scratch-line in the record.

I had been greatly puzzled by the triphasic electromotive response which sometimes appeared in the records. The presence of a highly excitable layer in the tissue would appear to offer an explanation of the phenomenon.

Experiment 98. *Effect of radio-thermal stimulation.*—The fact that triphasic response is universal is borne out by the record taken under radio-thermal stimulation T, applied on the upper half of the organ (fig. 93). The results are essentially similar to those in the previous experiment. The only difference is that on account of the stronger intensity of the stimulus the reversal to negative occurred somewhat earlier.

Experiment 99. *Effect of application of strong light on lower half of the pulvinus.*—The preliminary twitch was still erectile though the stimulus was applied below. Stimulation of the outermost layer initiated the positive impulse which, reaching the layer *c*, induced the erectile twitch. The excitatory contraction of the layers from *d* to *c* caused a slow fall of the leaf, which was next transformed into a very rapid fall by the contraction of the highly excitable and contractile layer *c* (fig. 94).

Thus, by the application of adequately sensitive physiological tests, the gradations of excitability in the interior of a tissue can be revealed.

Response of the Leaflet of Averrhoa

Diffuse stimulation induces a downward folding of the leaflet, proving that the excitability of the pulvinule is greater on the lower side.

Experiment 100. *Application of strong light from above.*—The response was a brief erectile movement, due to the contraction of the directly stimulated upper side of the

FIG. 95. Response of leaflet of Averrhoa to strong light from above.

organ; it was positively phototropic, *i.e.* movement towards the source of illumination. The response was subsequently reversed to strong negative in consequence of transverse conduction of excitation (fig. 95).

FIG. 96. Effect of strong light applied below (Averrhoa)

Experiment 101. *Application of strong light from below.*—The response was positively phototropic, that is, towards the source of illumination. As the more excitable lower side was directly stimulated, its predominant contraction was incapable of being neutralised by excitation transversely transmitted to the less excitable upper side (fig. 96).

Response of the Leaflet of Mimosa

Diffuse stimulation causes upward closure of the leaflet, proving that the excitability of the pulvinule is greater on the upper side.

Experiment 102. *Effect of strong light on upper side.*—The result is a very pronounced up-response, due to direct stimulation of the more excitable side, which was not reversed by transverse conduction of excitation to the lower less excitable side of the pulvinule (fig. 97).

Fig. 97. Fig. 98.

Fig. 97. Effect of strong light on upper side of Mimosa leaflet.

Fig. 98. Effect of strong light on lower side of leaflet.

Experiment 103. *Effect of strong light on lower side.*—A transitory down-response occurred, due to contraction of the directly stimulated lower side; this was subsequently reversed into a strong up-response by transverse conduction of excitation to the more excitable upper side (fig. 98).

These responsive manifestations find their fullest explanation in the previous experiments on the main pulvinus of Mimosa under the action of strong light, acting from above or below. Had a delicate means of record not been available, the gradual transition from positive to negative phototropic curvature would have passed unnoticed.

A continuity is thus established between phototropic and photonastic reactions, rendering the assumption of specific sensibility for each class of phenomena quite unnecessary.

The effects described are equally true of photic, thermal, and electric stimulations. From these results of observation and experiment on the movements of plants, the following laws, which are of universal application, can be deduced:

1. All forms of moderate or strong stimulation of organs in normal tonic condition induce contraction as their direct, and expansion as their indirect, effect.
2. The response to unilateral stimulation is a positive curvature, effected by contraction of the proximal and expansion of the distal side.
3. Transverse conduction of excitation induces contraction of the opposite side, consequently neutralising or reversing the positive responsive curvature.
4. These effects are accentuated by the differential excitability of the two halves of an anisotropic organ.

The fundamental reactions of pulvinated and growing organs to direct and indirect stimulation are summarised in the following table:

TABLE XVIII.—MECHANICAL AND ELECTRIC RESPONSES IN MOTILE AND IN GROWING ORGANS.

Inducing cause	Reaction	Mechanical response	Electric response
Direct stimulation	Contraction	Fall of leaf; negative response	Negative response
Indirect stimulation	Expansion	Erection of leaf; positive response	Positive response

I give a classification of some of the principal types of response to light that are met with in practice. In anisotropic organs, stimulus is supposed to be applied on the less excitable side.

1. Radial Organ.

   (a) Thick shoot; transverse conduction of excitation negligible; positive phototropic response, e.g. positive curvature.

   (b) Thin shoot or root; transverse conduction of excitation possible; sequence of responses: positive, neutral, and negative, e.g. reversal of positive into negative in stem of Oryza and in root of Sinapis.

2. Pulvinated Organ:

   (a) Pulvinus thick; transverse conduction of excitation negligible; positive response, pronounced concavity of the excited side. e.g. midday sleep or para-phototropism of *Erythrina indica*, *Clitoria Ternatea*, and others.

   (b) Pulvinus thin; transverse conduction of excitation pronounced; transient and hitherto unnoticed positive followed by predominant negative; application of stimulus on the opposite and more excitable side produces movement in the same direction, now positive response. The result would thus appear to be independent of the direction of light. Examples are found in the photonastic movements of the leaflets of *Mimosa pudica* and of Averrhoa and Biophytum.

Owing to varying combinations of numerous unknown factors the phenomena of growth and its responsive variations under stimulation present many perplexities. For instance, take the effect of external stimulus on growth. Here subminimal stimulus induces one effect, and moderate stimulus the very opposite. Should the tonic condition of the plant happen to be below par, the effect of stimulus will be an abnormal acceleration of growth, but during the course of the experiment (owing to the continued action of stimulus) the effect will mysteriously revert to the normal retardation. The point of application of stimulus will

introduce further complication, indirect stimulation inducing an effect precisely the opposite to that of direct stimulation. The response to unilateral stimulation is further modified by transverse conduction of impulse, by the intensity of stimulation, and by the differential excitability of the organ. In an actual experiment the permutation and combination of these different factors will give rise to effects which, no doubt, appear at first sight to be highly capricious. A given modification of response can, however, be traced to a corresponding definite variation in the intensity and point of application of stimulus, or in the tonic condition of the reacting organ.

The following is a diagrammatic representation of the typical cases in which an arrow represents the direction of incident light :

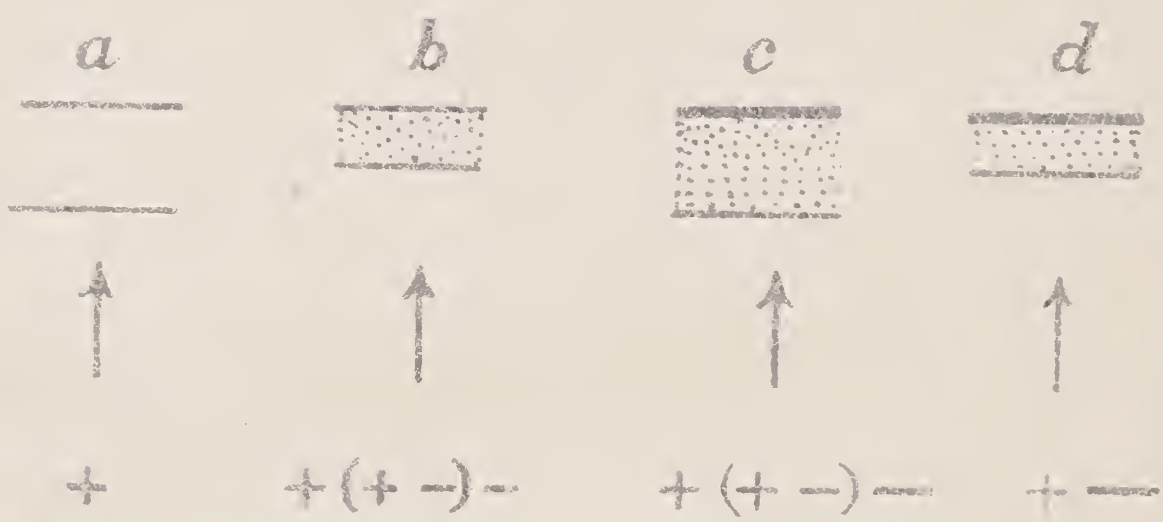


FIG. 99. Diagrammatic representation of different types of response to unilateral stimulation. Presence of dots represents possibility of transverse conduction.

+ represents positive curvature; + (+ –) – represents sequence of positive, neutralisation, and negative. Thick — represents predominant negative.

a, Radial thick organ. Transverse conduction absent. Response positive.

b, Radial thin organ. Sequence of response : positive, neutral, and negative.

c, Anisotropic thick organ. Thick line represents the more excitable distal side. Sequence of response : positive, neutral, and pronounced negative.

d, Anisotropic thin organ. High transverse conductivity. Sequence of response : positive quickly masked by negative.

When light strikes on the opposite side, the sign of response in *a* and *b* will remain unchanged. In *c* and *d* the effect will be only positive.

SUMMARY

By the application of sensitive physiological tests, gradation of excitability has been discovered in the layers of tissue in the pulvinus of Mimosa.

In an organ with pronounced physiological anisotropy, in which the distal lower is far more excitable than the upper or proximal side, stimulation of the proximal side is followed by a transverse conduction of excitation which brings about a greater contraction of the lower side. The sequence of response is then positive, neutral, and very pronounced negative. The terms proximal and distal are used in the sense of stimulated and unstimulated sides.

When the stimulus is applied on the more excitable lower side of the organ, the result is a predominant contraction of that half; the resulting curvature cannot be neutralised by transverse conduction of excitation to the feebly excitable distal side.

The phototropic and photonastic movements are not unrelated phenomena, but there is continuity between them.

CHAPTER XVI

RADIO-THERMOTROPISM

Tropic curvature induced by different rays of light has already been studied. It was found that while the more refrangible rays of the spectrum were most effective, the less refrangible rays were ineffective. Below the red there are the thermal rays, the effect of which is complicated by that of rise of temperature. The effects of these two factors are antagonistic, and to this must be ascribed the contradictory results that have been obtained by different observers, of which Pfeffer[1] gives the following summary:

'In addition to the action of ultra-red rays which are associated with the visible part of the spectrum, dark heat-rays of still greater wave-length, as well as differences of temperature, may produce a thermotropic curvature in certain cases. Wortmann observed that seedlings of *Lepidium sativum* and *Zea Mays*, as well as sporangiophores of Phycomyces, curved towards a hot iron plate emitting dark heat-rays. Steyer has, however, shown that the sporangiophore of Phycomyces has no power of thermotropic reaction. Wortmann observed that the seedling-shoot of *Zea Mays* was positively, but that of Lepidium negatively, thermotropic. . . . Steyer, however, found that both plants were positively thermotropic. Wortmann has also investigated the radicles of seedlings by growing them in boxes of sawdust, one side being kept hot, the other cold.'

It will be noted that in the investigations described above, thermotropic reaction has been assumed to be the

[1] Pfeffer, *ibid.* vol. iii p. 770.

same both under variation of temperature (as in experiments with unequally heated sawdust) and under radiation from a heated plate of metal. With reference to this Jost maintains that, 'so far as we know, thermotropism due to *radiant* heat cannot be distinguished from thermotropism due to *conduction*.'

The effect of temperature, within optimum limits, is physiological expansion and enhancement of the rate of growth (*cf.* fig. 15). The effect of visible radiation is, on the other hand, contraction and retardation of growth (*cf.* fig. 35). Should radiant heat act like light, the various tropic effects in the two cases would be similar; the temperature effect would in that case be opposite to the radiation effect. In order to ascertain if thermal radiation produces tropic curvature as does light, a crucial experiment has to be devised in which the complicating effect of rise of temperature on the responding organ is eliminated. Before referring to that experiment, I will describe the method of quantitative stimulation by thermal radiation.

RADIO-THERMAL STIMULATOR

This consists of a V-shaped loop of wire, heated short of incandescence by the passage of an electric current. The intensity of incident radiation can thus be maintained constant, and increased or decreased by approach or recession of the radiating loop. A series of thermal shocks can also be applied in rapid succession by means of a metronome, which closes the electric circuit (fig. 100).

I referred to the crucial test by which the complicating effect of rise of temperature on the responding organ can be eliminated. This experiment has already been described in Chapter XII (*cf.* fig. 67), in which radio-thermal stimulation was applied on the stem of Mimosa at a point opposite to the indicating leaf. The effect of unilateral stimulation of Mimosa by heat-rays was found to be exactly the same as

that induced by stimulation by light, *i.e.* there was at first an erectile movement due to indirect stimulation, followed by the fall of the leaf due to transverse conduction of excitation. The indicating leaf-organ was, in this case, completely shielded from the effect of rise of temperature.

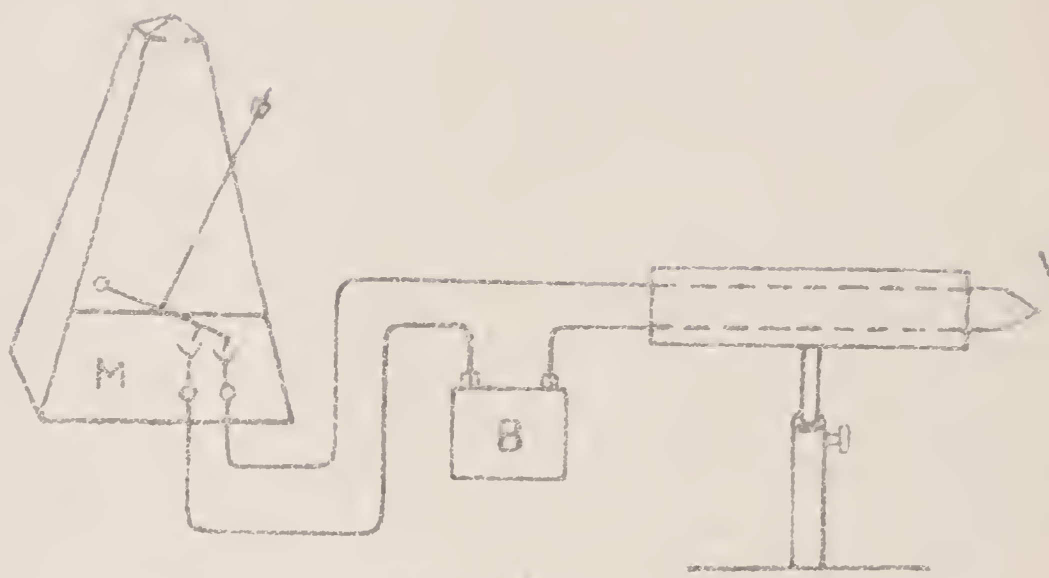


FIG. 100. Radio-Thermal Stimulator.

V-shaped loop heated short of incandescence by passage of electric current. Successive thermal shocks can be given by metronome.

Investigation has made it possible to establish a strict parallelism between the effects of luminous radiation and those of heat-radiation in inducing tropic curvature of plants. The experiments will be described in the following order:

1. The effect of indirect stimulation.
2. Positive radio-thermotropism.
3. Dia-thermotropism.
4. Negative thermotropism.
5. The response of the root to unilateral thermal radiation.

EFFECT ON GROWTH OF INDIRECT STIMULATION BY THERMAL RADIATION

The application of unilateral photic stimulation of moderate intensity at a distance from the growing region,

that is indirect sti[illegible] been shown to [illegible] negative curvature a[illegible] the stimulus [illegible] effective stimulation wa[illegible]r, a diphasic [illegible] occurred, a negative follo[illegible]ve (*cf.* fig. [illegible]).

Experiment 104.—A [illegible] experiment was carried out with the stem of a seedl[illegible] *[illegible]aba.* Application of unilateral thermal stimul[illegible] a distance of 6 cm. below the region of maximu[illegible] [illegible]oked a negative response, curvature away fro[illegible] [illegible]thus indicating

FIG. 101.   FIG. 102.

FIG. 101. Effect of indirect radio-thermal stimulation. [illegible]tion of application of stimulus between vertical line a[illegible] [illegible]orizontal arrow within circle. Negative response followe[illegible] [illegible]y complete recovery. (Vicia Faba.)

[illegible]2. Diphasic response of identical specimen under more [illegible]ective stimulation. Negative response followed by positive. (Vicia Faba.)

[illegible]tion of growth on the same side. This is seen in [illegible] (fig. 101); thermal radiation was applied at the [illegible] line and withdrawn at the horizontal arrow in [illegible] the total duration of stimulation being 40 seconds [illegible]d represents negative curvature; the move[illegible] [illegible] for a further period of 40 seconds, after [illegible]plete recovery.

Experiment 105.—The effective intensity of stimulation was next made stronger by reducing the intervening distance to 4 cm. The duration of stimulation was the same as before, namely, 40 seconds. The response was, as in the case of photic stimulation, diphasic negative curvature, followed by positive (fig. 102).

POSITIVE RADIO-THERMOTROPISM

Experiment 106.—The growing region of a stem was next stimulated unilaterally for a short time by thermal radiation.

FIG. 103. Positive response to stimulation by short exposures to thermal radiation. Successive dots at intervals of 5 seconds (Dregea volubilis).

Fig. 103 gives a record of response of the stem of Dregea; the induced curvature is positive or towards the source of heat. On the cessation of stimulation, there is a recovery which is practically complete, and which takes place at a slower rate than the excitatory positive curvature. Repetition of stimulation gives rise to responses similar to the first. *Successive stimulations of moderate intensity thus give rise to repeated responses of positive growth-curvature.*

Experiment 107. *Response of pulvinated organ.*—In order to show that thermal radiation is an effective stimulus

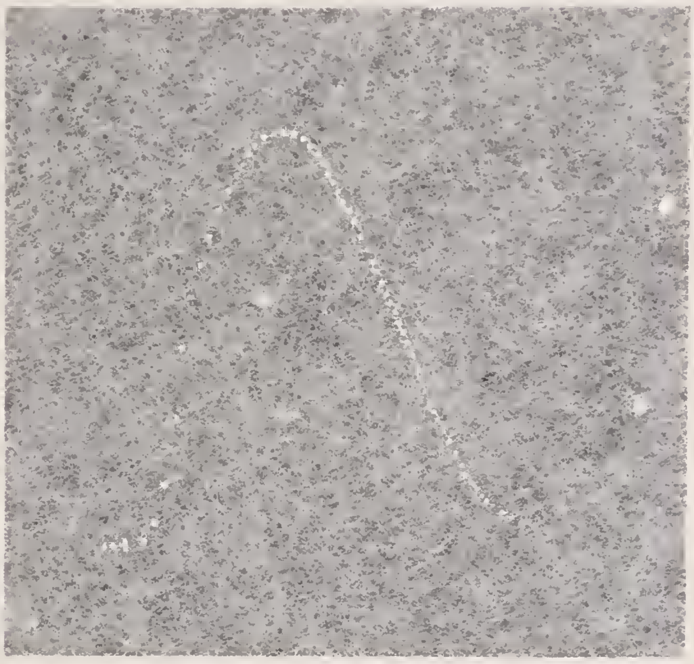


FIG. 104. Response of pulvinus of Mimosa to thermal radiation.

for a motile organ, I reproduce the response of Mimosa to the rays of heat (fig. 104).

DIA-THERMOTROPISM

I shall henceforth use the shorter term *thermotropism* to indicate tropic curvature under unilateral action of thermal rays. In the case of photic stimulation, it has been explained how the positive curvature is induced by retardation of growth at the proximal side and enhancement of growth at the distal side, this latter being the effect of indirect stimulation by transmitted positive impulse.

But under long-continued action of stimulus the negative or excitatory impulse reaches the distal side, inducing diminution of turgor and retardation of the rate of growth. This leads to neutralisation, the organ placing itself at right angles to the direction of orienting stimulus.

Experiment 108.—Neutralisation is seen in the record given in fig. 105, where under continuous unilateral stimulation the growing stem of Dregea exhibited its maximum

positive curvature, after which the movement became arrested by the arrival of the excitatory impulse at the

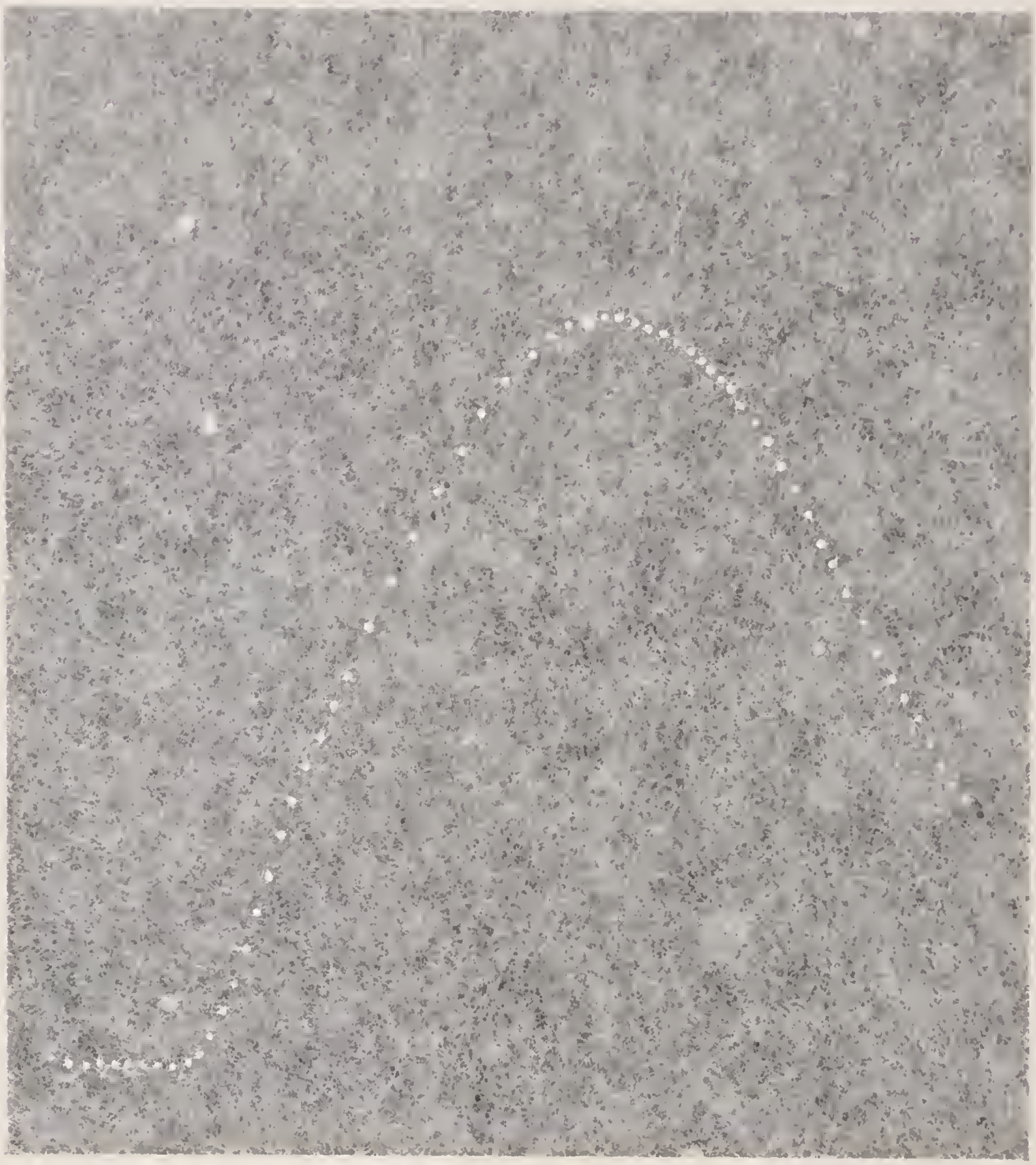


FIG. 105. Record of positive, neutral, and negative curvature under continued unilateral action of thermal radiation. The negative response went off the plate. Successive dots at intervals of [illegible] seconds. (Dregea volubilis.)

distal side, on account of which the positive curvature became neutralised. Further continuation of the stimulation caused a reversal into negative in the course of 7 minutes.

NEGATIVE THERMOTROPISM

Experiment 100.—The response does not stop at neutralisation but proceeds further, ending in reversal; that is, to pronounced negative curvature by the contraction of the distal side due to conduction of excitation, and to

fatigue-relaxation of the proximal side. As the thermal radiation is relatively more effective than light, the reversal, generally speaking, occurs much earlier. I have obtained numerous records in confirmation; the second part of the record (fig. 105) is, however, sufficient to illustrate this. After neutralisation the curve is seen to undergo a reversal indicating negative thermotropic curvature.

It is interesting to note in this connection that in the phototropic curvature induced by sunlight the heat-rays play as important a part as the more refrangible rays of the spectrum.

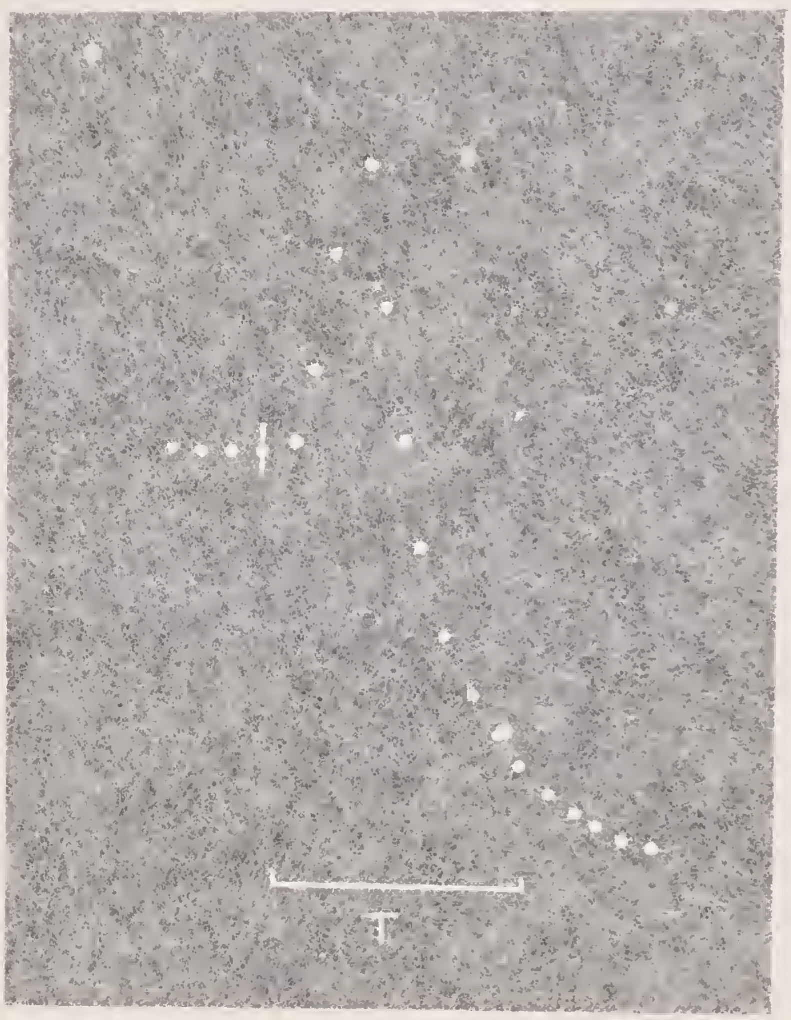


FIG. 106. Response of root to unilateral and continuous thermal radiation, T. Positive, neutral and negative curvature. (Ipomoea reptans.)

The Response of the Root

It has been shown that under unilateral action of light a root exhibits first a positive, then a neutral, and finally a negative movement. This last phase is exhibited under very prolonged exposure (p. 145). The advantage of thermal radiation is, as already explained, the relatively greater effectiveness of the stimulus on account of which the three stages can be observed within a shorter period.

Experiment 110.—I reproduce a record given by the root of *Ipomoea reptans* under unilateral thermal radiation. The latent period was 10 seconds, and the posit

curvature continued for 40 seconds. Neutralisation then occurred, after which the tropic curvature became reversed into a very pronounced negative (fig. 106).

SUMMARY

The effects of rise of temperature and of radiation are antagonistic to each other.

The response to unilateral stimulation by thermal radiation is a positive curvature induced in both shoot and root by the retardation of growth at the proximal, and acceleration of growth at the distal, side of the organ.

There is complete recovery on the cessation of stimulation of moderate intensity and short duration. Repeated responses may therefore be obtained similar to the repeated responses of pulvinated organs.

In certain cases the power of conduction in a transverse direction is wanting; excitation remains localised at the proximal side, and the responsive curvature remains positive. In other cases there is a slow conduction of excitation to the distal side. The result of this under different circumstances is dia-radio-thermotropic neutralisation, or even a negative curvature.

The heat-rays in sunlight play as important a part in inducing phototropic curvature as the more refrangible rays of the spectrum.

The root, under unilateral action of thermal radiation, exhibits positive, neutral, and negative curvature, as it does under unilateral photic stimulation.

CHAPTER XVII

RESPONSE OF PLANTS TO WIRELESS STIMULATION

A GROWING plant bends towards the light, and this is true not only of the main stem but also of its branches and the attached leaves and leaflets. It has already been shown how light affects growth, the effect being modified by the intensity of radiation. Strong stimulus of light causes retardation of the rate of growth, but a very feeble stimulus induces acceleration. The tropic effect is very strong in the more refrangible region of the spectrum with its extremely short wave-length, but the effect declines practically to zero towards the less refrangible rays—the yellow and the red. Proceeding beyond the infra-red region, there comes the vast range of electric radiation, the wave-lengths of which vary from 0·6 cm., the shortest wave I have been able to produce, to others which may be miles in length. There thus arises the very interesting question whether plants respond to the long ether waves, including those employed in signalling through space.

At first sight this would appear to be very unlikely, for the rays known to be the most effective are in the blue-violet region with wave-length as short as 30×10^{-6} cm., whilst the electric waves used in wireless signalling are 50 million times as long. The perceptive power of the human retina is confined within the very narrow range of a single octave, the wave-lengths of which lie between 70×10^{-6} cm and 35×10^{-6} cm. It is difficult to imagine that plants could respond to radiations so widely separated from each other as those of visible light and those of invisible electric waves.

It is the less refrangible rays which are most active in the building-up process of photosynthesis. The dynamic and potential manifestations are thus complementary to each other, the rays which induce photosynthesis being relatively ineffective for tropic reaction and *vice versa*.

The less refrangible yellow-red rays have been shown to be phototropically ineffective. Proceeding further into the infra-red region of the thermal rays, it has been shown that they become suddenly effective in causing retardation of growth and in inducing tropic curvature. A curve drawn with the wave-length of light as abscissa, and the effectiveness of the ray as ordinate, shows a fall towards zero in proceeding from the violet to the red; the curve, however, shoots up in the region of the infra-red. Does the effectiveness of the rays for inducing tropic reaction abruptly end with the thermal rays, or does it persist, though in a lesser degree, in the region of the electric radiation, the wave-length of which is enormously greater?

It should be borne in mind that the energy of the electric waves which reach the plant from a distance is relatively feeble, and hence its effect is likely to be slight and detectable only by an extremely delicate method of record, and by the employment of highly sensitive specimens.

Before proceeding further with the subject of the possible effect of wireless waves on the plant, I thought it desirable to find out whether or not a rapidly alternating electric field of force has any effect on the plant.

Response of Plant to High-Frequency Alternating Field of Electric Force

The investigation was undertaken to find whether the plant, placed within the influence of the field generated by high-frequency and high-tension alternating current, exhibited any responsive reaction. The investigations were carried out with Mimosa as well as with growing plants.

Experiment 111. *Effect of alternating field on Mimosa.* For the high frequency alternating current I employed a

small portable set known as the 'violet-ray apparatus.' It was not difficult to get a marked response when the so-called violet ray emitted by one of the electrodes struck the plant. But being desirous of obtaining the pure effect of the high-frequency electric field, I had a large hollow spiral placed in series with the secondary of the Tesla coil. The pulvinus and petiole were placed inside the spiral,

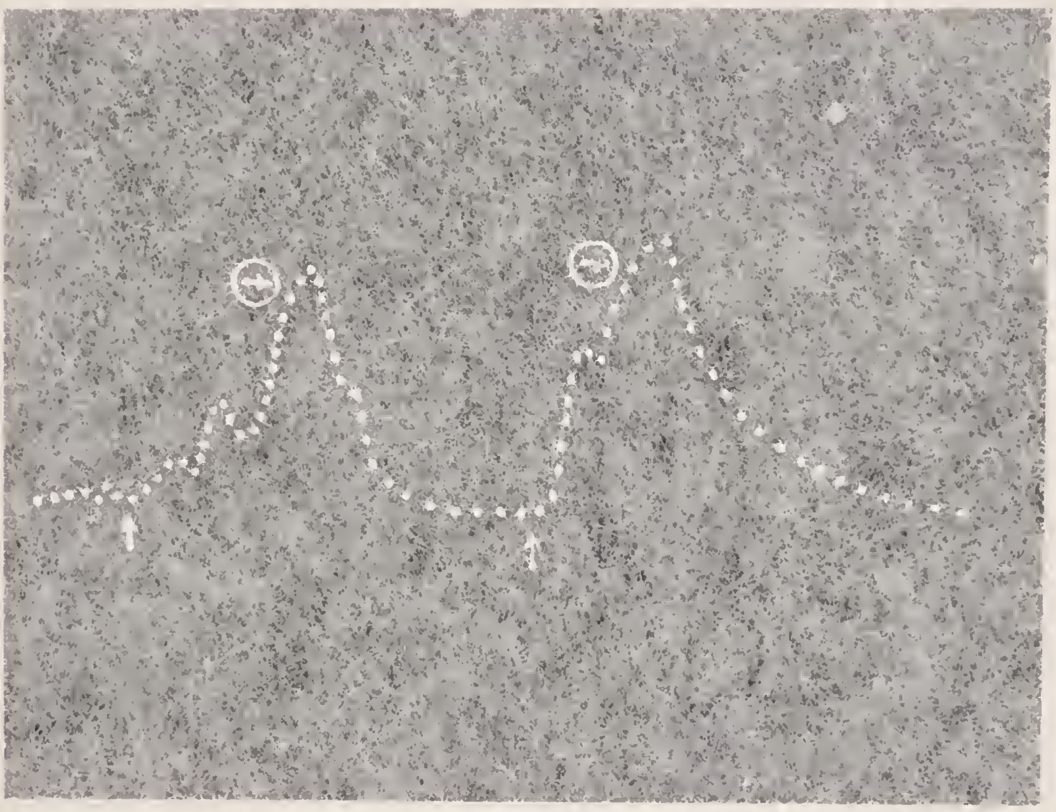


FIG. 107. Effect of high-frequency alternating electric field on response of pulvinus of Mimosa.
Note slow contractile fall with minute pulsations.
Arrow indicates moment of stimulation, arrow within circle its cessation.

a portion of the petiole projecting out of it for connection with a recorder.

With a very sensitive specimen of Mimosa the response was an excitatory fall, the responsive reaction being induced within 10 seconds of the incidence of the stimulus. The contraction in this case was slow and gradual as under the action of light, and not abrupt as under an electric shock. The contraction persisted for a time after the cessation of stimulation, after which there was a gradual recovery (fig. 107).

Effect of alternating electric field on growing organs.—The experiments were carried out under two different methods of producing the alternating field. In the first method two insulated plates are connected with the terminals of the secondary coil, the plant being placed between the two. The intensity of the stimulation is in this case less than when the plant is placed in the interior of a spiral.

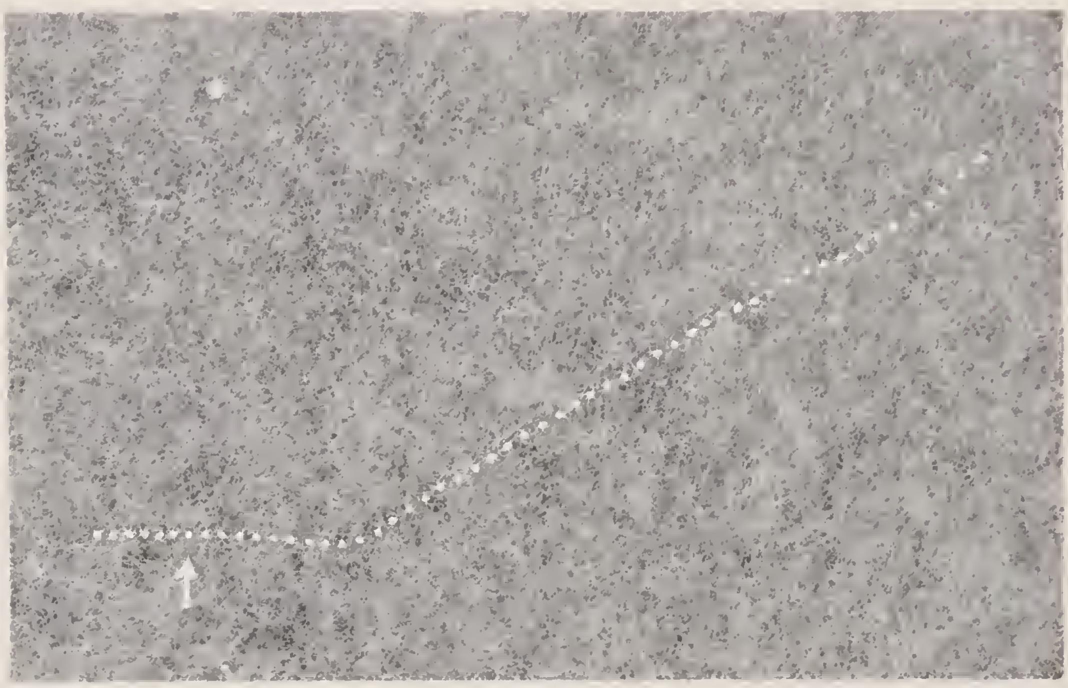


FIG. 108. Effect of high-tension alternating field on growth.

Acceleration (up-curve) under moderate stimulation (Wheat). Record under condition of balance. Successive dots at intervals of 10 seconds.

Experiment 112.—A seedling of Wheat was chosen for this experiment, its rate of growth being relatively feeble (0·19 μ per second). The specimen was mounted on the Balanced Crescograph, the horizontal line at the beginning showing the record under condition of balance. On subjecting the plant to the action of the alternating field of moderate intensity at the point marked with arrow, the balance was upset within a minute and a half of the application of stimulus. There was an acceleration of growth as exhibited by the up-curve (fig. 108). Another Wheat-seedling was so subtonic that growth was at a standstill, the record being horizontal without balance. The high-

frequency electric field was found to initiate growth, which persisted for a considerable length of time (fig. 108A)

Experiment 113. *Effect of strong stimulation.*—I next took another seedling of Wheat which exhibited a more active rate of growth, of 0·5 μ per second. The effective intensity of stimulation was increased by enclosing the plant within a spiral, as in the experiment with Mimosa. The result was a marked retardation of growth exhibited

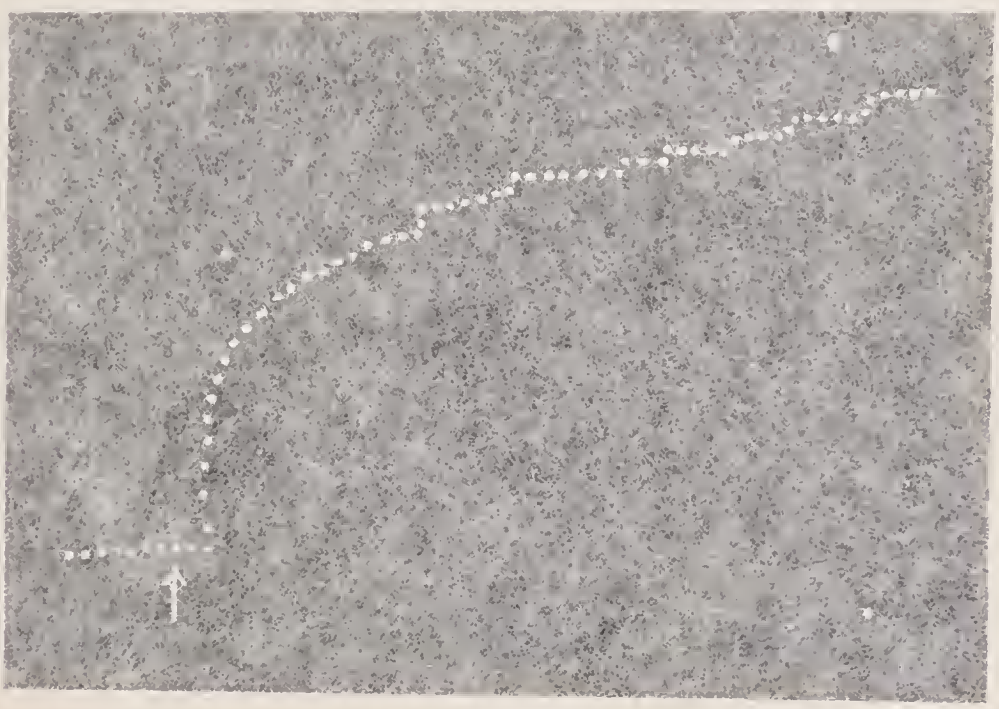


FIG. 108A. Revival of growth in Wheat-seedling in condition of standstill.
Normal record, without balance

by the down-curve, the balance being upset within 30 seconds of the incidence of stimulus (fig. 109). The results prove that *the effect of high-tension alternating current on growth is determined by the intensity of stimulation, and by the tonic condition of the plant.* A subtonic organ under feeble stimulation exhibits, in general, acceleration of growth, while an actively growing organ under strong stimulation shows retardation. These characteristics are such as have been found under other modes of stimulation.

The effects of high-tension alternating current on growth, as noticed by different observers, have been found to be very contradictory. The facts described above on the

modifying influence of tonic condition and intensity of stimulation will probably afford an explanation of the anomaly.

I now describe the effect of wireless waves on growth

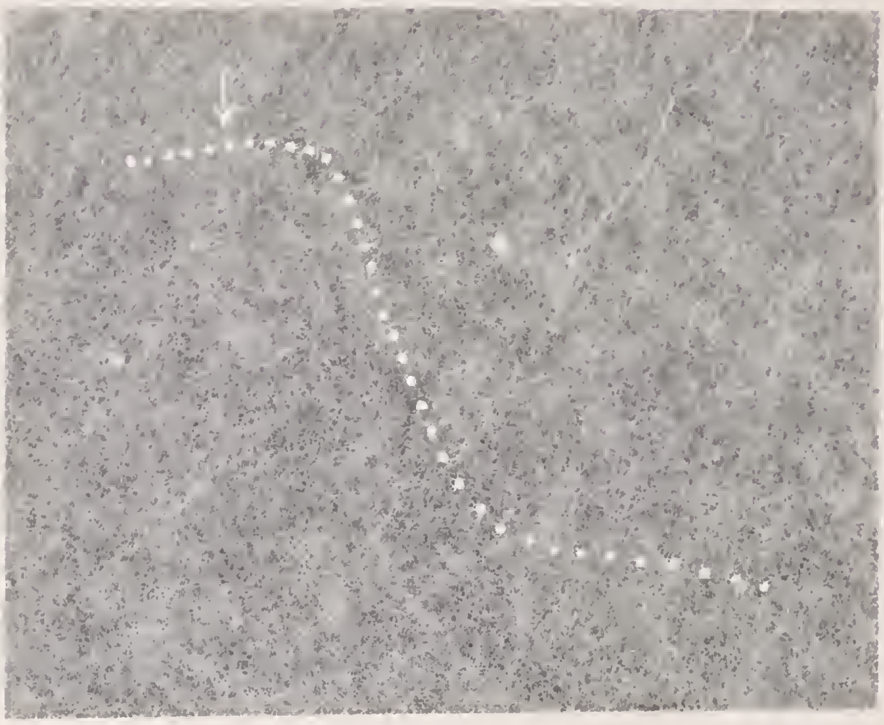


FIG. 109. Effect of strong intensity of field in retarding growth (Wheat).
Record under condition of balance.

THE WIRELESS SYSTEM

For sending wireless waves, I had to improvise the following arrangement, more powerful means not being available. The secondary terminals of a moderate-sized Ruhmkorff's coil were connected with two cylinders of brass, each 20 cm. in length; the sparking took place between two small spheres of steel attached to the cylinders. One of the two cylinders was earthed, and the other connected with an aerial 10 metres in height. At the receiving end the aerial was connected by means of a thin wire with the experimental plant growing in a pot, which was put in electric connection with the earth (fig. 110). The distance between the transmitting and receiving aerial was about 200 metres, the maximum length permitted by the grounds of the Institute.

I describe a typical experiment on the effect of wireless waves on the growth of a seedling of Wheat. The specimen was mounted on the Balanced Crescograph, and the growth

exactly balanced. This gave a horizontal record; an acceleration of growth above the normal is represented in the records by a down-curve, and a retardation by an up-curve.

Experiment 114. *Effect of feeble stimulation.*—I first studied the effect of feeble stimulation secured by decreasing the energy of the sparks of the radiator. The response was

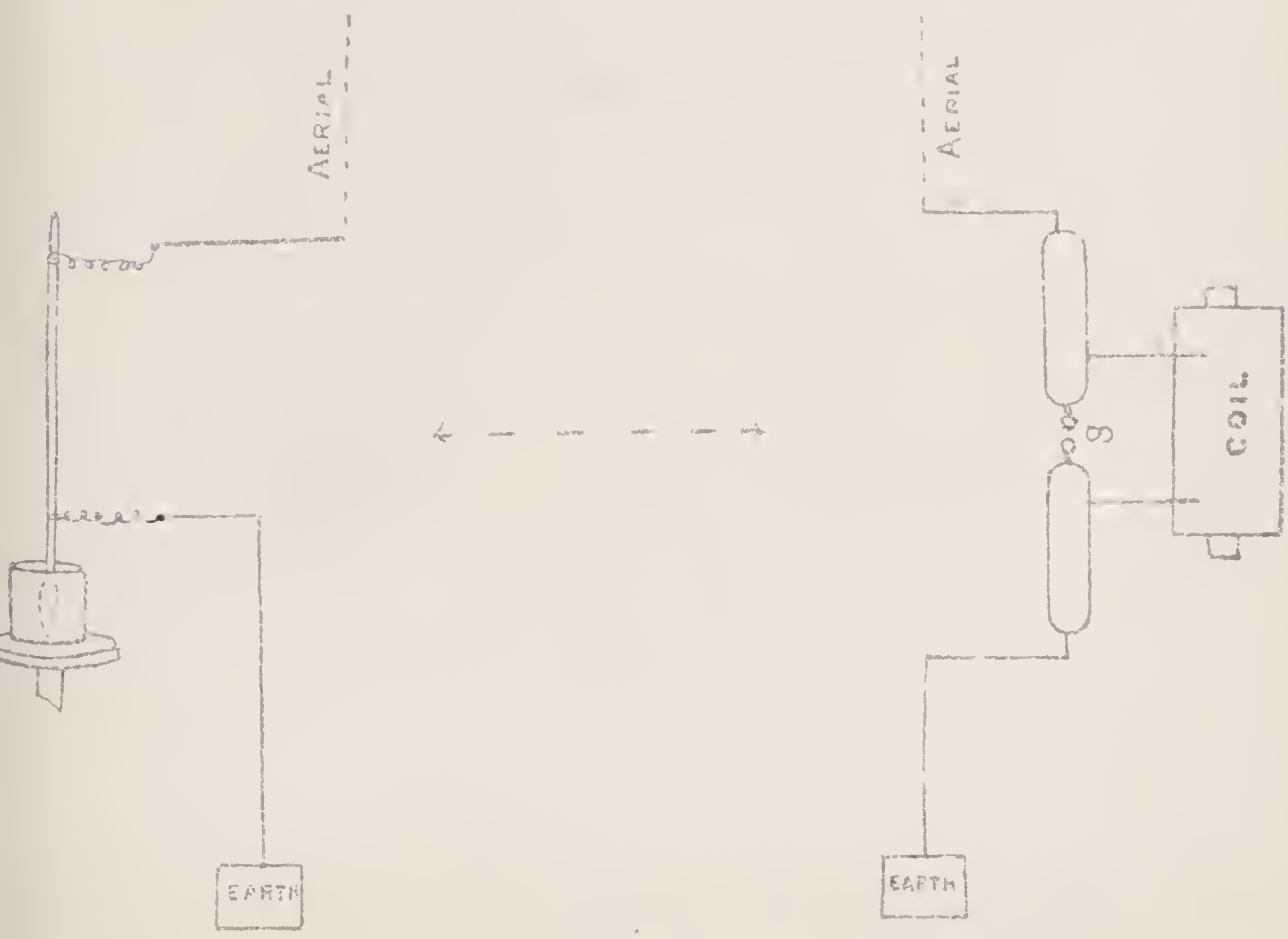


FIG. 110. Diagrammatic representation of method employed for obtaining response to Wireless Stimulation. Transmitting apparatus seen to the right. Receiving aerial connected to upper part of plant, the lower part of the plant or the flower-pot being connected with the earth.

an acceleration of rate of growth as seen in fig. 111, *a*. The analogy of this with the accelerating effect of subminimal intensity of light (p. 83) is very remarkable.

Experiment 115. *Effect of strong stimulation.*—The maximum energy radiated by my transmitter, as stated before, was only moderate. In spite of this, its effect was very striking on plants in good tonic condition. The balance was quickly upset, indicating retardation of the rate of growth. The latent period, *i.e.* the interval between

the incidence of the wave and the response, was only a matter of a few seconds in very sensitive specimens (fig. 111, *b*). The record given in the figure was taken with the moderate magnification of 2000 times only. But with my Magnetic Crescograph the magnification can easily

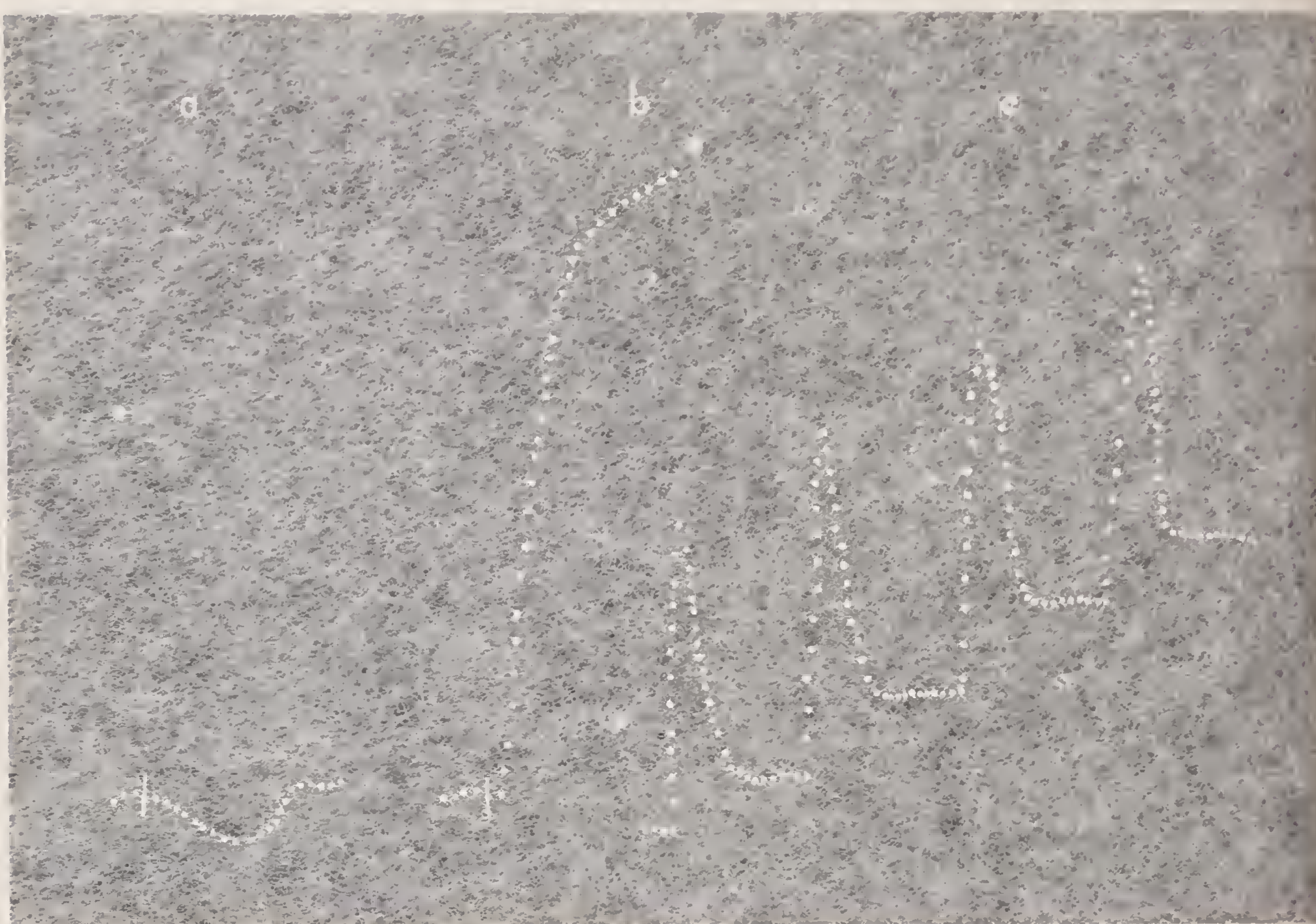


FIG. 111. Record of responses to electric wave with the Balanced Crescograph.

a, Response to feeble stimulation by acceleration of growth (down-curve).
b, Response to strong stimulation by retardation (up-curve).
c, Response to medium stimulation—retardation followed by recovery. Note down-curve in this figure represents acceleration, and up-curve retardation of growth. (Wheat.)

be raised to ten million times, and the response of the plant to space-signalling can be increased in the same proportion.

Under an intensity of stimulation slightly above the minimal, the responses exhibit retardation of growth followed by recovery, as seen in the series of records (fig. 111, *c*).

A remarkable peculiarity in the response was noticed during the course of the experiment. Strong stimulation by ether waves gives rise, as already stated, to marked retardation of the rate of growth. Repeated stimulation

induced fatigue and temporary insensitiveness of the organ. The effect of moderate fatigue is a prolongation of the latent period. Thus, in a particular experiment the plant failed to give any response to a short signal. But after an interval of 5 minutes a marked response occurred to the wireless stimulation that had been previously received. The latent period was prolonged, on account of fatigue, from a few seconds to as many minutes. In less sensitive specimens the wireless stimulation has to be continued for several minutes in order to evoke response.

EFFECT OF WIRELESS WAVES FROM A PORTABLE GENERATOR

A short-wave four-valve set adjusted to send out wireless oscillations of definite wave-length was used. Just

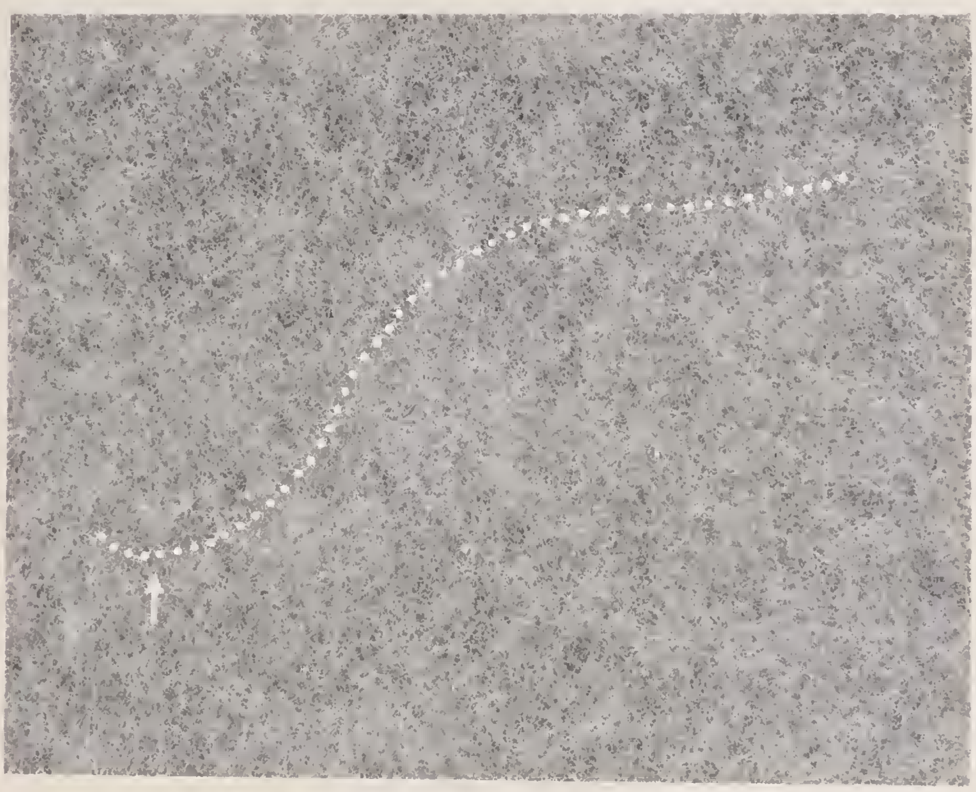


FIG. 112. Acceleration of growth by wireless stimulation in a subtonic specimen (Wheat).

Enhancement of growth in this and following records represented by up-curve, retardation by down-curve. Successive dots 20 seconds apart.

Record taken under condition of approximate balance.

before application to the plant the transmitter was tested by the receiver to make sure that wireless waves of a particular

frequency were being produced, the reading dial having been calibrated beforehand. Employing the portable generator for electric waves, I succeeded in repeating most of the results given above. The energy of radiation emitted was not very great; the length of the wave was about a metre.

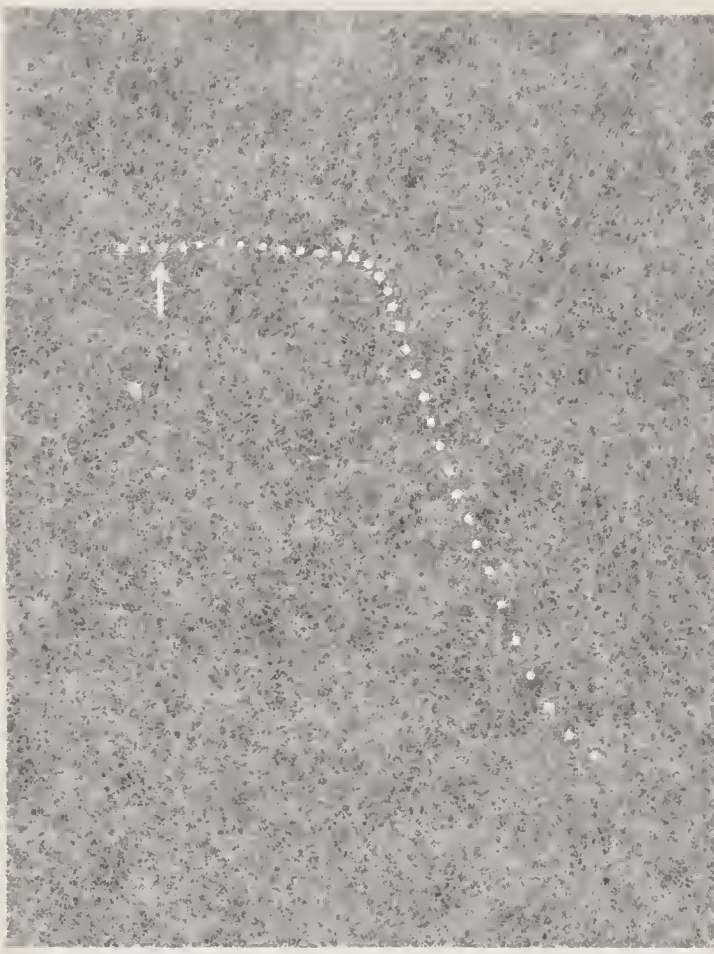


FIG. 113. Retardation of rate of growth under strong wireless stimulation (Crinum).

Record taken under condition of balance.

I give the following typical results obtained with the portable generator.

Experiment 116. *Acceleration of growth in a subtonic specimen.*—The specimen of Wheat-seedling exhibited the feeble rate of growth of 0·37 μ per second. Wireless stimulation induced an acceleration of the rate of growth. The stimulus was relatively feeble, and the enhancement of response, as exhibited by the upsetting of the balance in an upward direction, occurred shortly after the application of stimulus (fig. 112).

Experiment 117. *Effect of moderately strong stimulation on actively growing organ.*—A peduncle of Crinum Lily exhibited a moderately active rate of growth (0·40 μ per second). It was subjected to wireless stimulation, which induced a retardation of the rate of growth, shown by the down-curve (fig. 113). The upsetting of the balance, showing diminished rate of growth, occurred about 3 minutes after the incidence of stimulus.

Experiment 118. *Record of growth-variation without balance.*—An interesting and confirmatory experiment was

carried out with a seedling of *Zea Mays*, the record being taken without balance. The up-curve at the beginning exhibits the normal rate of growth (0·49 μ per second).

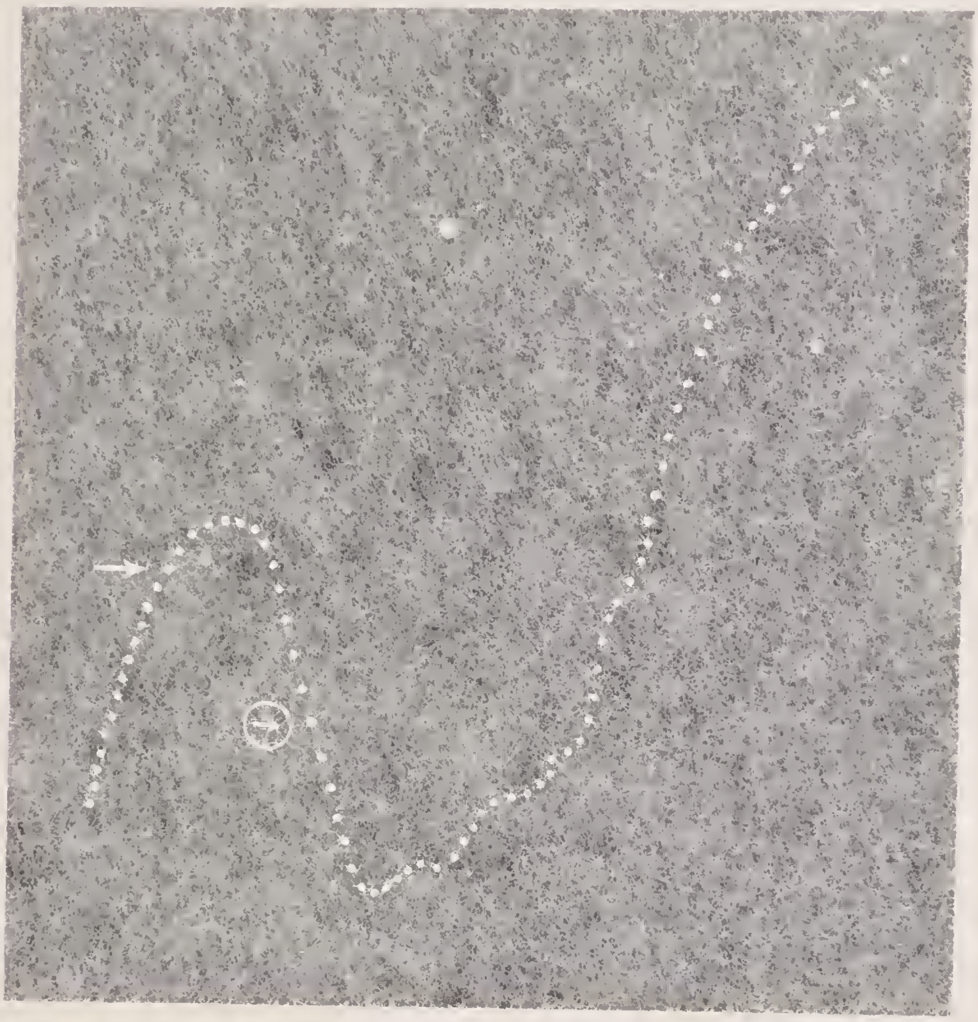


FIG. 114. Effect of wireless stimulation: unbalanced growth. Up-curve of growth reversed to contractile down-curve followed by slow recovery (Zea Mays).

Application of stimulus at the horizontal arrow induced a contraction exhibited by the reversal of the curve 80 seconds after the application of stimulus. On the cessation of stimulation the normal rate of growth was gradually restored (fig. 114).

SUMMARY

Pulvinated and growing organs exhibit response to a high-frequency alternating field of electric force.

The response is modified by the tonic condition of the organ and the intensity of stimulation.

In response to wireless waves, growing plants exhibit modification of their rate of growth. Feeble stimulation induces an acceleration, while strong stimulation causes a retardation of the rate of growth, as has already been shown to be the case in response to other forms of stimulation.

CHAPTER XVIII

DIURNAL MOVEMENTS OF PLANTS

THE most diverse and complicated movements of different organs of plants occur in response to variations of the environment, notably when the external conditions undergo a periodic change. The plant is subjected, day and night, to variation of illumination, to change of temperature, and to change of turgor caused by the difference between the accession of water by the root and loss by the transpiring leaves. The organs of plants are, moreover, subjected to the stimulus of gravity, the effectiveness of which varies with the angle of inclination of the organ to the vertical.

The plant, as already stated, is affected by many forms of stimulation acting simultaneously. The phenomena of plant-movement have remained obscure on account of the numerous factors which contribute to induce them. This is sufficiently illustrated by the consideration of but two out of the agents which affect the plant—the stimulus of gravity and that of light. Certain organs are highly sensitive to geotropic stimulation, while others are but feebly sensitive to it. The stronger reaction may be represented by G and the feeble by g. In regard to light, there are two distinct classes of reaction: *positive phototropism*, when the organ turns towards the light; and *negative phototropism*, when the organ turns away from it. These reactions when strong will be represented by $+L$ and $-L$; when feeble, by $+l$ and $-l$.

What will be the resulting effect when a horizontal stem is exposed to combined geotropic and [illegible]

stimulation? Under geotropic action the stem will tend to curve upwards; should it be positively phototropic, the curvature under vertical light will also be upwards. Geotropism and phototropism will thus conspire, the joint effect being $G + L$; but should the organ be negatively phototropic the result would be $G - L$. If further account be taken of the reactions of the organ to feeble and strong stimulations of gravity and light, the following combinations are possible:

$$G + L;\ G - L;\ G + l;\ G - l.$$
$$g + L;\ g - L;\ g + l;\ g - l.$$

Eight different effects can thus be produced by the combination of only two factors; there are, however, other factors active, such as the rise and fall of temperature. Additional complications are introduced by the unequal sensitiveness of the two sides of the organ; in some it is the upper side, in others it is the lower side that is the more excitable and therefore reacts more effectively. There are thus at least ten factors in operation, and the different combinations possible would exceed a thousand.

It is therefore not surprising that the movements of plants appear so extraordinarily complex. Efforts to discover a real explanation have long been baffled by the fact that it has hitherto been impossible to isolate and study the effect of each of the factors for the final analysis of the complex result.

In the consideration of the diurnal movements of plants in general, the following subjects will be treated in detail:

1. Daily movements in relation to light and darkness.
2. Diurnal movements due to variation of temperature affecting growth.
3. The diurnal movements of the 'Praying' Palm.
4. The effect of variation of temperature on fully grown organs subjected to the stimulus of gravity.
5. After-effect of light.
6. The complex diurnal movement of the leaf of Mimosa.

The diurnal movements of plants are generally due to the recurrent changes of light and darkness and to variation of temperature, the resulting movement being due to the algebraical summation of their individual effects. In regard to these two factors, the effect induced by the rise of temperature is often antagonistic to that of increasing intensity of light; a rise of temperature enhances the rate of growth up to an optimum, whereas light acts as a stimulus, retarding the normal rate of growth. Variation of temperature, moreover, affects the organ as a whole, whereas light may act unilaterally, depressing the rate of growth of the particular side subjected to light.

For a full analysis of the diurnal movements of plants, it thus becomes necessary to obtain a continuous record throughout every hour of the day and night of:

1. The movement of the plant-organ;
2. The variation of temperature; and
3. The change in the intensity of light.

In the next chapter I describe in detail the Automatic Recorder for the diurnal movements of plants, the variation of the temperature being also recorded by the Thermograph on the same recording plate. The far more difficult problem of the automatic record of variation of light will be dealt with in the present chapter.

The Self-Recording Radiograph

The method adopted for obtaining a record of the variation of intensity of light depends on the characteristic property of the selenium cell, which exhibits a diminution of its electric resistance under illumination. When a selenium cell is placed in the dark, in series with a battery of voltaic cells, it gives a small deflection of the galvanometer in circuit; illumination causes an increase of this deflection, according to the intensity of light. Several difficulties are, however, encountered in the practical application of this

method for obtaining a continuous record for the whole day. The resistance of the selenium cell undergoes a change due to polarisation under the continued action of the electric current; but this can be rendered negligible by maintaining a feeble current for a very short time. The variation of temperature at different periods may also affect the resistance of the selenium cell. This will be shown to be very slight and practically negligible. The most difficult problem is the automatic record of the galvanometric deflection under changing intensity of light.

The complete Radiograph consists of:

1. The Wheatstone Bridge for balancing the electric resistance of the selenium cell in the dark, the balance being upset on exposure to light.
2. The arrangement of three electric keys which are automatically put on and off in regular sequence and at predetermined intervals.
3. The Self-Recording Galvanograph.

The Wheatstone Bridge.—This is diagrammatically represented in B (fig. 115). The resistance of the particular selenium cell S is 76,000 ohms in the dark. An approximately equal resistance is placed in the second arm of the bridge. A rheostat having a large number of turns of fine wire with a sliding contact is used for the two variable arms of the bridge, diagrammatically represented by a straight line. An approximate balance is obtained when the sliding contact is in the middle; a slight movement to the right or to the left secures the exact balance, when the galvanometer deflection is reduced to zero. The balance is upset when the selenium cell is exposed to light, and the resulting deflection gives a measure of the intensity of the light.

The Automatic Keys.—After previous adjustment of the balance in the dark, the electric circuit is completed by the closure of key K_1, after which the selenium cell is exposed to light by an automatic electro-magnetic shutter. The deflection of the galvanometer is recorded on a piece of

moving paper by means of electric sparks. These different operations are carried out in proper sequence by the automatic devices described below.

K_1 completes the battery circuit for about 10 seconds, by which time the record is completed. The successive

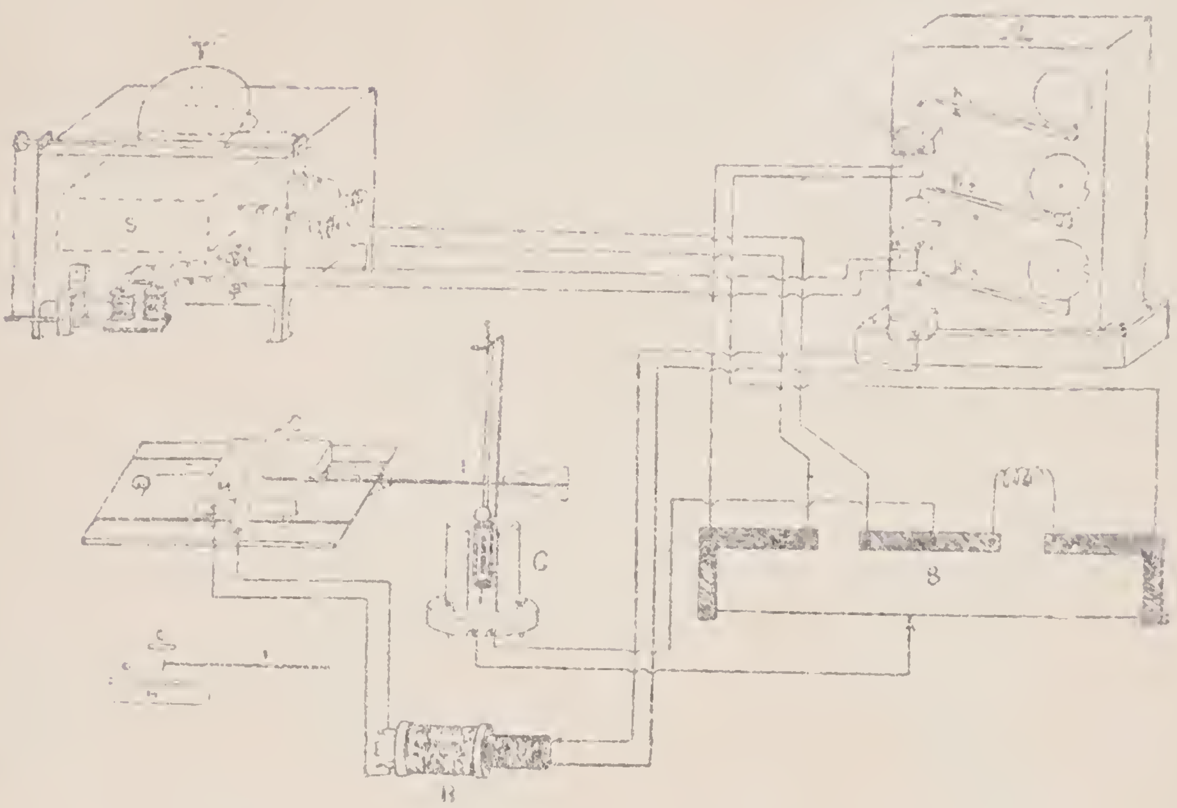


FIG. 115. The Self-Recording Radiograph.

The selenium cell, S, is periodically exposed to light by the electro magnetic shutter, T. The selenium cell forms one arm of the Wheatstone Bridge, B. The three keys, K_1, K_2, K_3, are periodically closed and opened by clockwork. G, the recording galvanometer with index, I, carrying double pointed sparking platinum wire, which moves between the metal strip C and the plate M. R, sparking coil with its electrode connected with C and M. The battery is not shown in the figure (*see* text).

records of variation of light are taken at intervals of 15 minutes; the periodic closures of the circuit are thus for 10 seconds at intervals of 15 minutes. In practice this short passage of the current is found to cause no polarisation.

The second key, K_2, actuates an electro-magnetic device by which the trap-door T is opened for the definite period of 1 second; the selenium cell, S, inside the dark box is thus exposed to light for this length of time. The trap-door

is shown in the diagram immediately above the dark box. In reality it is at the upper end of a vertical tube, the inside of which is coated with lamp-black to prevent side reflection. The light that falls on the selenium cell is thus from a definite area of the sky. The intensity of light from the sky at different periods of the day causes deflection of the galvanometer which is proportional to that intensity. The maximum deflection of the galvanometer employed is attained in the course of 3 seconds after exposure.

The third key, K_3, is for the completion of the spark-circuit for record of the maximum galvanometric deflection 3 seconds after the exposure of the selenium cell. This key actuates a sparking coil, R, the vibrating interrupter of which is not shown in the figure. The spark thus produced punctures the maximum deflection of the galvanometer index on a moving piece of paper attached to the plate M.

The successive closure and opening of the keys are made automatically and in proper sequence by means of clock-work, the whole process being repeated at intervals of 15 minutes.

The Galvanograph.—Now comes the most difficult problem—the automatic record of the galvanometer deflections. A record may be secured without great difficulty by means of photography. A spot of light reflected from the galvanometer mirror may be allowed to fall on a photographic plate which descends at a uniform rate by clock-work. This, however, entails the use of a dark room and subsequent development of the plate. This trouble was avoided by the device of direct record of the galvanometer deflection by means of electric sparks.

A sparking method has been previously employed in which the deflected index of the galvanometer in connection with one electrode of an induction coil leaves a spark-record on a moving piece of paper. Several difficulties are, however, encountered in the employment of this method with a highly sensitive galvanometer. There is a liability of leakage of the high-tension current into the galvanometer

circuit; also the discharge of the spark gives a backward kick to the index, by which the normal deflection undergoes an unknown variation.

These difficulties were removed in the following manner: The moving coil of the sensitive D'Arsonval galvanometer has a long glass index I at right angles to the plane of the coil, the index being coated with shellac varnish to render it highly insulating. It projects for a short distance on the opposite side for attachment of a counterpoise, which takes the form of a vertical vane of mica acting as a damper. The galvanometer itself is of an aperiodic type, and the addition of the damper makes it perfectly dead-beat. The sensitiveness of the galvanometer is such that a micro-ampere current produces a deflection of 10 mm. of the index. The recording index has attached to it a short vertical piece of thin platinum wire pointed at its two ends; the index moves between the sheet of metal M, covered with paper for record, and a semicircular piece of narrow sheet-metal C. The metal sheet M is mounted on wheels and moves at a uniform rate by clockwork. One electrode of the sparking coil is in connection with C, and the other with M. The sparking thus takes place simultaneously, above and below the vertical and double-pointed platinum wire carried at the end of the index. There is thus no resultant kick, and the index remains undisturbed. The sparking, as previously stated, takes place 3 seconds after exposure of the selenium cell to light, by which time the deflection reaches its maximum. The record thus consists of successive dots at intervals of 15 minutes, the dots representing the maximum deflections of the galvanometer corresponding to the intensity of light.

The record given in fig. 116 was taken about the end of January; the sun rose at about 6.45 A.M. and set at 5.30 P.M. Twilight is very short in the tropics; the sky is feebly lighted about 6 A.M. The record shows the intensity of light to be exceedingly feeble at 6 A.M. The rise in the intensity was rapid, attaining the maximum at 12 midday,

which will be designated as the light-noon. The intensity of light then declined at a rate slower than the rise. But after 5 P.M. the fall of intensity was extremely rapid.

An important point arises in connection with the diurnal variation of light and of temperature, and determination of

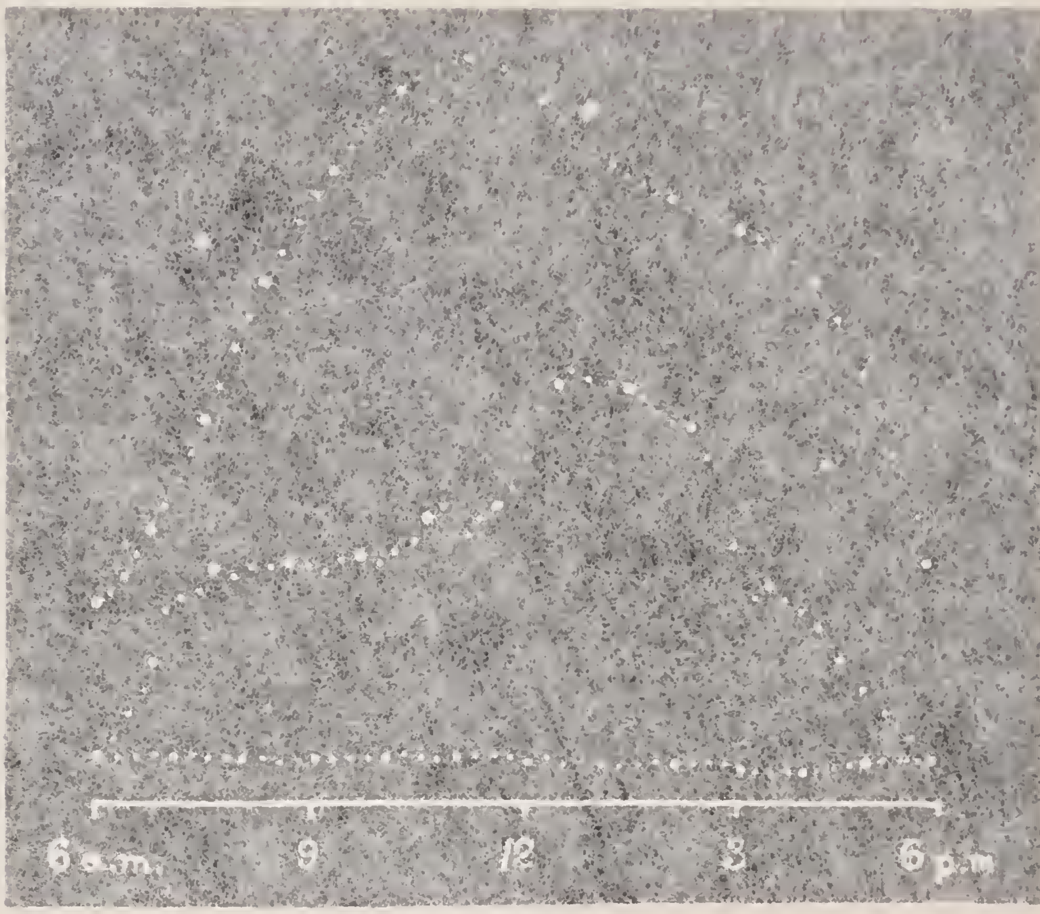


FIG. 116. Radiogram of variation of intensity of light from the sky during 12 hours in winter. The upper record shows the variation on a bright day, the maximum intensity being attained at 12 midday. The lower record exhibits irregular variation on a cloudy day. The horizontal record above the base line shows that the electric resistance of the selenium cell is practically unaffected by variation of temperature. Successive thin dots at 15 minutes interval, thick dots at intervals of an hour.

the times of their maxima and minima. For this purpose records of diurnal variation of temperature and of light were taken on the same day in summer with the Thermograph (described in the next chapter) and the Radiograph. The two curves are given in fig. 117.

It will be seen that while the maximum intensity of light is at 12 noon, the thermal maximum is at about 2 P.M. The thermal noon is thus two hours later than the light-

noon. Light disappears at night from 6 P.M. to 6 A.M., that is to say, the period of minimum light is prolonged for 12 hours. But the fall of temperature is gradual, and the minimum is attained at or about 5 A.M., which is the thermal dawn. The characteristic variation of these two important factors should be borne in mind, since the diurnal movements of plants are modified by the algebraical summation of the effects of light and of temperature.

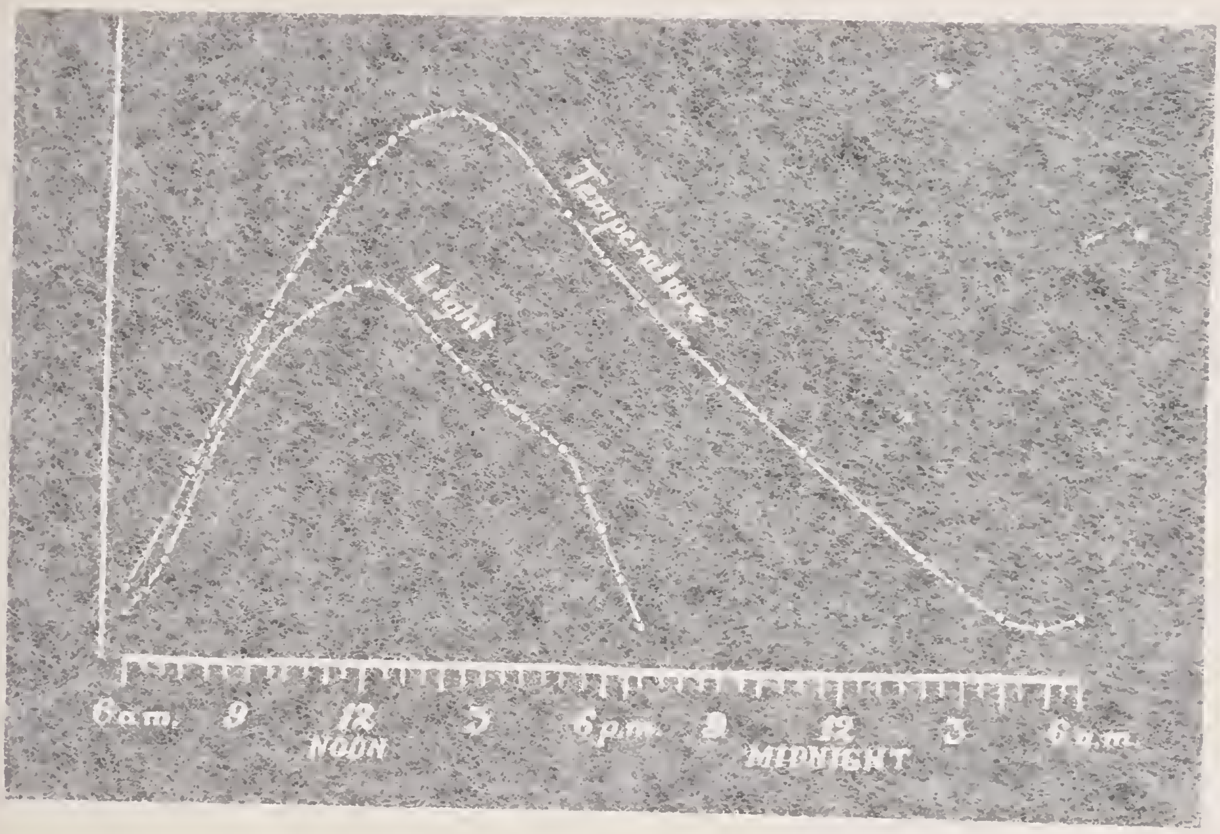


FIG. 117. Record of diurnal variation of light and of temperature in summer.

It is sometimes desirable to carry out researches during a period when the intensity of light remains approximately constant. Such a period occurs between 11 A.M. and 1 P.M., for a variation is only ± 5 per cent. of the mean.

The record given of the diurnal variation of light is true of days when the sky is clear. But the passage of a cloud causes change in the intensity which is accurately recorded by the Radiograph. A record of such irregular variation on a stormy day is given in the lower record of fig. 116.

For facility of treatment of the diurnal movement of

plant-organs, I shall consider the three ideal types: (1) where variation of light is the most important factor; (2) where the movement is principally due to differential growth under variation of temperature; and (3) where a fully grown tree at an inclination to the vertical, and therefore subjected to the stimulus of gravity, exhibits up or down movement under variation of temperature.

The determination of the isolated effect of any one individual factor, difficult as it is, can be arrived at by a process of judicious elimination. Thus the predominant effect of light, of variation of temperature, or of geotropic action can be inferred more or less from the following observations.

Predominant effect of light and darkness.—The obvious method of observing the effect of keeping the plant in continuous darkness presents the difficulty that the tonic condition of the plant is greatly depressed, resulting in the abolition of its normal irritability under prolonged darkness. The effect of withdrawal of light can therefore be satisfactorily observed only for about two days in succession.

The characteristic effect of light is very marked at two definite times of the day, when light appears and when it disappears. The average dawn is approximately at 6 A.M., and the average sunset at 6 P.M.; unlike the diurnal variation of temperature, which is gradual, the change from light to darkness or from darkness to light is relatively abrupt. Since the change of temperature and of light are both connected with the appearance and the disappearance of the sun, some difficulty arises in discriminating the effect of one from that of the other.

Light and temperature effects.—Light appears in the morning, say, at 6 A.M.; it becomes most intense at noon; after 4 P.M. the light wanes and darkness sets in quickly after 5 P.M. and remains persistent till next morning. The course of variation of temperature is somewhat different. The minimum temperature is attained at about 5 A.M. in summer, and at about 7 A.M. in winter. The maximum

temperature is reached at about 3 P.M. in summer, and about 1 P.M. in winter. The range of daily variation in summer may be taken to be between 23° C. and 38° C., in winter between 16° C. and about 29° C. These are the normal variations and not the sudden fluctuations that occur during uncertain weather conditions.

The temperature remains constant for nearly an hour during the period of transition from falling to rising temperature, and *vice versa*. The average time of minimum temperature may be taken to be at 6 A.M., which I distinguish as the thermal dawn; the maximum temperature, the thermal noon, is attained at about 2 P.M. Variation from these average times at different seasons does not amount to more than an hour.

Light dawn and thermal dawn are more or less coincident, while thermal noon is two hours later than light noon. A change in the diurnal curve of movement, due to thermal variation, will thus be detected at about 2 P.M. If the curve of daily movement of the plant-organ closely resembles the diurnal thermographic curve, there can then be no doubt of the causal relation of variation of temperature in the production of the periodic movement.

The effect of geotropism can be detected, as will be explained later, by taking the record of the plant in normal and in inverted positions.

Summary

The phenomena of the diurnal movements of plants are greatly complicated by the algebraical summation of the effects of numerous factors. The most important of these are the effects of light and darkness, of variation of temperature, and of thermal variation on organs subjected to the action of gravity.

In order to trace the effects of the more important individual factors, it is necessary to obtain continuous record of variation of temperature by the Thermograph, of variation

of light by the Radiograph, and of the corresponding movement of the plant-organs by the Plant-Recorder.

The Radiograph gives a record of the diurnal variation of light. On a clear day in January the intensity was found to increase rapidly from 6 A.M. to 12 noon, when it reached its maximum. Light began to decline slowly up to 5 P.M., the decline being less rapid than the rise in the forenoon. The fall of intensity was extremely rapid after 5 P.M. Any fluctuation of light, due even to a passage of a cloud, is accurately recorded by the Radiograph.

The individual effects of the main factors can be to some extent discriminated from each other. The contrasted effects of light and darkness are most pronounced in the morning when light appears, and in the evening when light disappears. A pronounced flexure in the diurnal curve at these periods indicates the predominant character of the action of light. The effect of light can also be distinguished from that of temperature from the fact that the period of maximum intensity of light, or light-noon, is about 2 hours earlier than the thermal noon, at which the temperature is maximum.

A flexure of the diurnal curve about thermal noon, at which an inversion takes place from rise to fall of temperature, indicates the effect of temperature. The additional test of the effect of temperature is furnished by the close resemblance between the diurnal curve of the plant and the thermographic record for 24 hours.

CHAPTER XIX

EFFECT OF RECURRENT LIGHT AND DARKNESS ON MOVEMENTS OF PLANTS

FOR the demonstration of the effect of recurrent change of light and darkness in the course of day and night, the experimental plants must be such as have organs which readily respond to photic stimulation. One of these is the leaf of *Cassia alata*, the petiole of which carries a

FIG. 118. Leaflets of Cassia alata: open in daytime, and closed in evening.

number of paired leaflets, each of which is about 5 cm. long and 2·5 cm. broad. At night each pair of leaflets fold themselves in a forward direction (fig. 118). With the appearance of light they open at first in a lateral direction; later on there is a twist of the pulvinus by which the inner surface of the leaflets faces light coming from above. The diurnal movements of the leaflets will be shown to be due to the predominant effect of variation of light.

It will be convenient to begin with a general description of the experimental methods employed, and of the apparatus by which diurnal movements are recorded.

Experimental Arrangements

When the diurnal record has to be taken continuously for several days in succession, it is necessary to take precautions

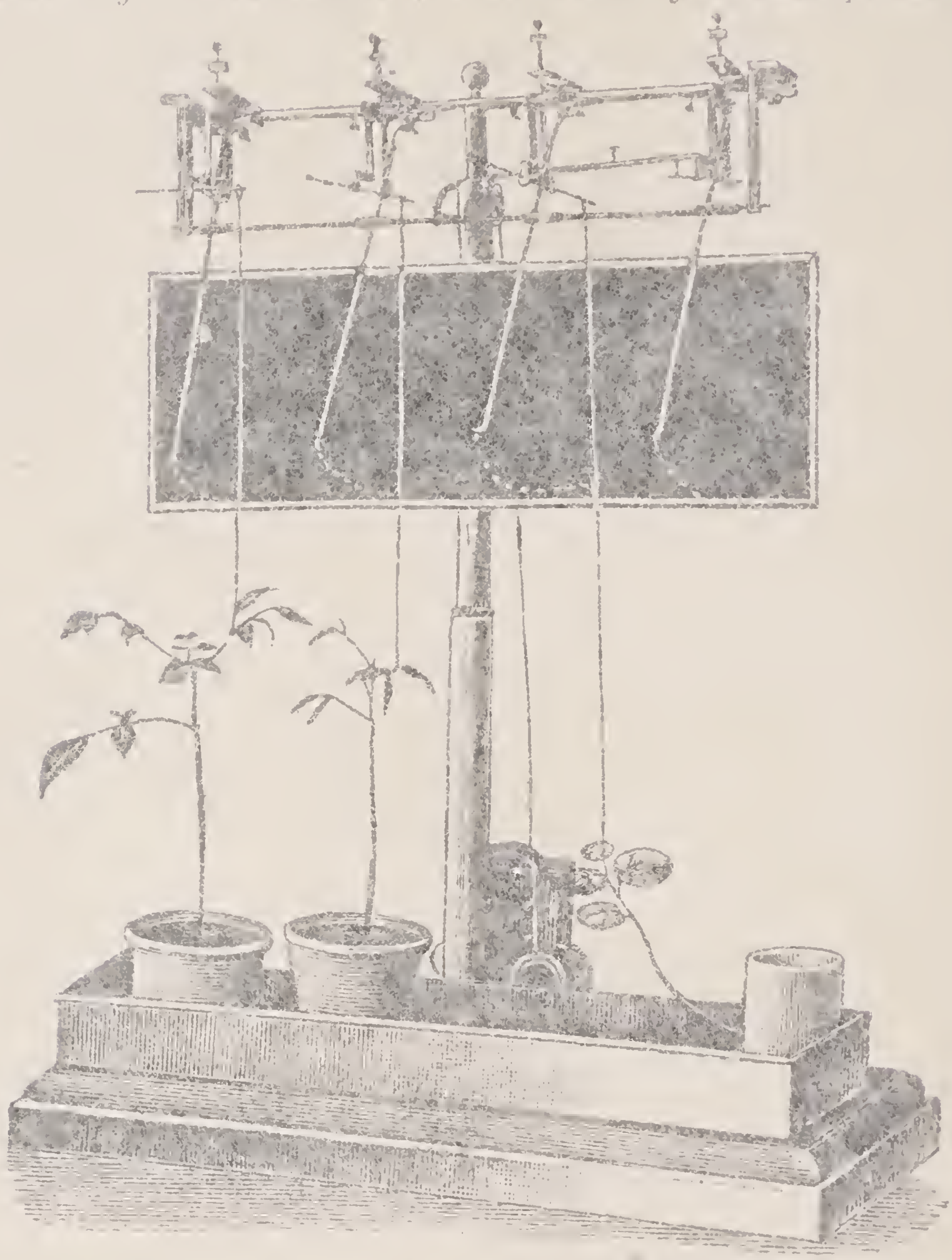


Fig. 110. The Automatic Recorder of diurnal movements of plants. Quadruplex form provided with four writing levers. The flower-pots are placed in a trough filled with water to a constant height. The first two levers are shown in the figure to record movements of leaves, the third to record movements of a horizontally laid shoot; the fourth lever, attached to a differential thermometer, T, records diurnal variation of temperature.

against the disturbing effect of watering the plants, and of tropic curvature of the stem induced by one-sided illumination.

[simult]aneous records under identical external conditions [of leav]es of different age of the same plant, or of leaves [of] different species. I have for several years past [taken re]cords of numerous plants and at all seasons of the [year. T]he plant's autograph is often so characteristic that [I am a]ble to name it by mere inspection of its daily record.

[T]hermograph.—For obtaining a continuous record of [the v]ariation of temperature, I use a compound strip, [made] of brass and steel. Variation of temperature [induces c]urvature of the compound strip, which is recorded [by mea]ns of an attached lever. The oscillation of the plate [takes p]lace once in 15 minutes, and the successive dots [thus pro]duced give time records of the diurnal curve. The [record t]hus consists of a series of dots. An additional [device so]metimes employed is to make the plate oscillate [several tim]es in rapid succession at the end of each hour; [the hourl]y dot is thus thicker than others. The movement [of the pla]nt-organ corresponding to any particular variation [of tempe]rature at any period may thus be easily deter[mined]. I shall now give a typical example of diurnal [movemen]t induced by variation of light and darkness.

[RE]SPONSE OF THE LEAFLET OF CASSIA ALATA

[The] leaflets remain tightly closed during the night, but [from ear]ly morning onwards they begin to open and remain [fully s]pread out throughout the day. The problem is to [find] the relative importance of variation of temperature [and li]ght in the diurnal movement of the leaflets.

[In th]e daytime the light is increasing till midday; [there is,] on the other hand, a rapid decline of light after [noon a]nd uninterrupted darkness during the night. As [to te]mperature there is a continuous rise from morning [till t]hermal noon, after which the fall of temperature [contin]ues till next morning. The opening of the leaflets [in day]time will therefore be due to the summated effects [of rising] temperature and increasing light; the closure in

Irrigation.—There is, as is well known, a periodic ... tion of turgor which is disturbed by watering the pl... irregular intervals. Precaution against this was ... placing the flower-pots containing the plants in ... trough filled with water (*see* fig. 119). The height ... in the trough is maintained constant by a syphon ...

Vertical illumination.—The direction of sunlight ... from morning to evening and the stem and leaves ... appropriate movements under the changing dire... light. In order to obviate this, a special chamb... constructed which allowed light from the sky ... vertically on the plant through a sheet of groun... which covered the roof, the light thereby becoming u... diffused. The sides and the base of the chambe... impervious to light, the plant was protected fro... illumination. A narrow slit covered with red glass ... inspection of the curve during the process of record.

The Ventilator.—A revolving ventilator, acted ... the wind, sucked the air away from the chambe... ensuring a constant supply of fresh air without ... any disturbance of the record.

AUTOMATIC RECORD OF DIURNAL MOVEMENT

The Recorder.—The Oscillating Recorder empl... of the quadruplex type carrying four recording ... (fig. 119). The function of the apparatus is to ... various types of diurnal movement. The fourth lever ... the daily variation of temperature: the other th... attached to plants of either the same or different s... In the former case three records are obtained of th... species of plant under identical external conditions. ... agree in all essentials, the periodic curve may be ... as characteristic of that particular species. A ver... saving of time is thus ensured, and it is therefore p... to obtain characteristic curves of numbers of di... species of plants within the short period of a s... The quadruplex recorder also permits the obta...

the evening, on the other hand, will be due to falling temperature and to darkness. The individual effect of each of these factors is not known, and it is therefore necessary to determine the relative effects of variation of temperature and of light.

Effect of Variation of Temperature

Experiment 119.—The plant was enclosed in the glass chamber and the experiment was commenced at midday, when the leaflets were open, under uniformly diffused light. The temperature was artificially raised by means of an electric heater placed in the chamber, and lowered by the introduction of cold air. One of the leaflets was attached to the recording lever, and its movement, up or down, indicated the opening or closing movement of the leaflet. The records showed that rise of temperature induced a movement of closure, while fall of temperature brought about a movement of opening.

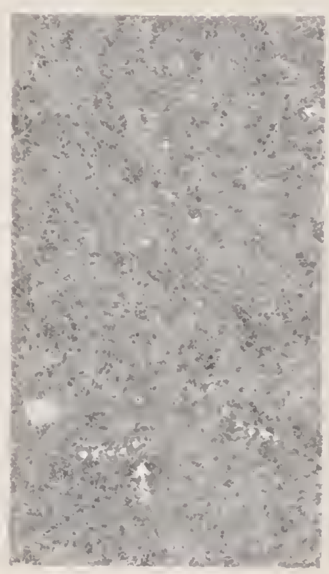


Fig. 120. Effect of sudden darkening at arrow producing movement of closure (up-curve). Restoration of light induces movement of opening (down curve). Successive dots at intervals of 15 minutes. (Leaflet of Cassia.)

Effect of Variation of Light

Experiment 120.—This experiment was also carried out at midday, when the leaflets were fully open. The horizontal part of the record in fig. 120 represents the stationary expanded condition of the leaflet; a black cloth was put over the glass chamber at 1 P.M., and the effect of darkness was recorded for one hour. Darkness is seen to have initiated a movement of closure which increased at a rapid rate, the black cloth was then removed, and the movement of opening under light was completed in the course of five quarters of an hour. A passing cloud causes an immediate movement of closure, proving how very sensitive is the leaflet to variation of light.

The effects of rise of temperature and of light have been shown to be antagonistic to each other. The opening movement under light in the forenoon has to be carried out against the closure-tendency due to rise of temperature. Light, therefore, is the predominant factor in the diurnal movement of the leaflet of Cassia. The closure-effect of darkness at night, on the other hand, overpowers the tendency to movement of opening due to fall of temperature.

Diurnal Movement of the Leaflet of Cassia alata

Experiment 121.—I next took the diurnal record of the leaflet from 4 P.M. till 1 P.M. next day. As the leaflets were open previously from 1 P.M. to 4 P.M., the record of this

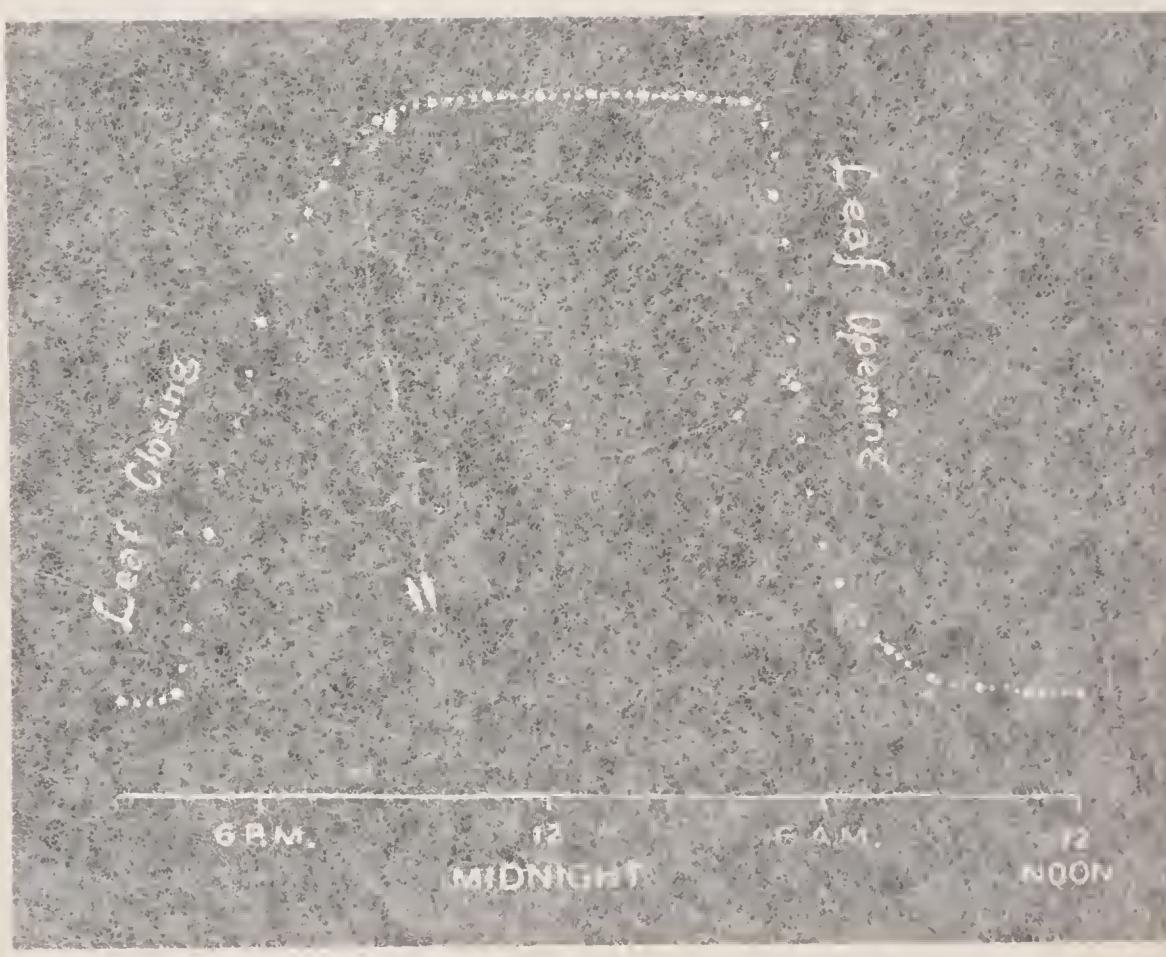


FIG. 121. Diurnal movement of the leaflet of Cassia alata. Closure-movement commenced at 5 P.M. and was completed by 9 P.M. Leaflet began to open at 5 A.M.

period is omitted. In the diurnal record (fig. 121) the first thick dot was made at 4 P.M., successive thick dots are at intervals of an hour, the thin dots being at intervals of 15 minutes. It will be seen that a rapid movement of

closure was initiated at 5 P.M., when the light was undergoing rapid diminution. The movement of closure was completed at about 9 P.M. The leaflets remained closed till 5 A.M. next morning, after which they began to open; this opening may commence even an hour earlier. It should be borne in mind in this connection that since light and rise of temperature are antagonistic in their reactions, the effects of light and of fall of temperature would be concordant, and the opening in the early hours may possibly be hastened by the low temperature in the morning. The leaflets were open to their utmost by 9 A.M., and they remained open till the afternoon.

Another interesting example of the diurnal movement due to variation of light is found in the terminal leaflet of *Desmodium gyrans*, an account of which is given below.

DIURNAL MOVEMENT OF THE TERMINAL LEAFLET OF DESMODIUM

Both the petiole and the terminal leaflet of this plant exhibit a very marked nyctitropic movement. In the

FIG. 122. The day and night positions of the petiole and terminal leaflet of Desmodium gyrans.

evening the petiole is raised and becomes almost erect, while the terminal leaflet exhibits a sharp curvature downwards (fig. 122).

Experiment 12.—The petiole was held fixed, and the terminal leaflet was attached to the recording lever. Under natural conditions, daylight acting from above induces an up-movement; darkness, on the other hand, induces a rapid movement of fall. The leaflets sometimes exhibit autonomous pulsations; but the diurnal movement is very strong, so that the daily curve appears as a single large pulse on which smaller autonomous pulsations may be superposed.

The diurnal curve (fig. 123) exhibits a sudden fall at about 5 P.M., resulting from the rapid waning of afternoon

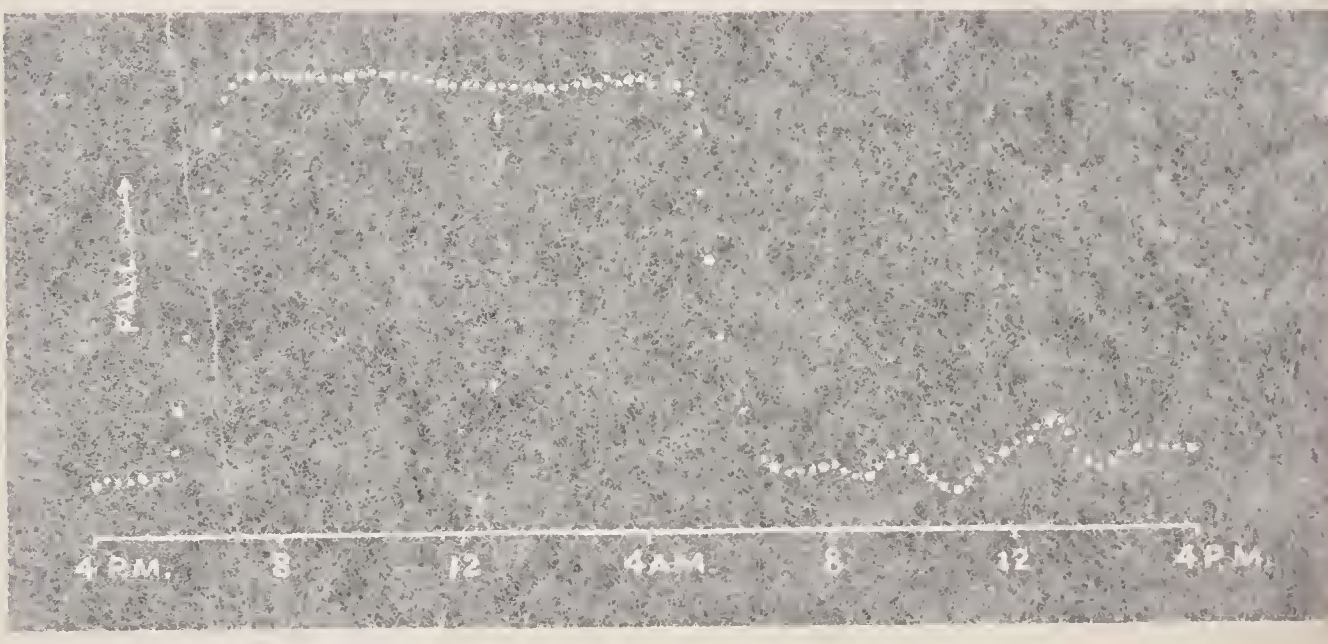


FIG. 123. Record of diurnal movement of the terminal leaflet of Desmodium gyrans. Up curve represents down-movement.

light, till by 6.30 P.M. the leaflet becomes closely pressed against the petiole.

The question arises whether or not variation of temperature has any marked effect on the diurnal movement of the leaflet. It has been explained that when an organ of a plant is sensitive to variation of temperature, the record exhibits a flexure at about 2 P.M., when there is a change from rise to fall of temperature. No such flexure was, however, observable at that period. But the sensibility of the leaflet to variation of light is seen in the rapid closure movement about 5 P.M. The leaflet remains tightly closed throughout the night, and begins to open and spread out

early in the morning at about 5 A.M. This up-movement is also very rapid, and the leaflet assumes its fullest outspread position by 7 A.M. It remains in this position till the afternoon, after which the cycle is repeated. As the leaflet is very sensitive, the position of equilibrium of the leaflet is liable to be disturbed by the slightest fluctuation of light from the sky, which often gives rise to a wavy outline in the record. The leaflet, moreover, has a tendency to exhibit rhythmic pulsations.

In the leaflets of Cassia and Desmodium the daily movements are determined by light rather than temperature, the plant being more responsive to the former than to the latter.

Summary

Rise of temperature induces a movement of closure of the leaflet of Cassia, fall of temperature inducing the opposite movement.

Artificial darkness induces a movement of closure, re-exposure to light brings about the opening of the leaflets. These are so extremely sensitive to light that closure-movement is induced by the transitory passage of a cloud.

The effect of rise of temperature is antagonistic to the action of light. The movement of opening during the course of the day is due to the response to light overpowering the response to rise of temperature

Under daily variation of light and darkness the movement of closure is initiated at about 5 P.M., when the light is undergoing rapid diminution. The movement of closure is complete by 9 P.M. The leaflets remain closed till about 5 A.M. next morning, when they begin to open and become fully expanded by 9 A.M.

The terminal leaflet of Desmodium exhibits a diurnal movement which is very similar to that of the leaflet of Cassia. It begins to open early in the morning and remains outspread during the day; it exhibits a rapid down-movement after 5 P.M. and becomes closely pressed against the petiole in the course of about 2 hours.

CHAPTER XX

THERMONASTIC MOVEMENT OF NYMPHAEA

THE term 'nastic' is convenient when employed in the restricted sense as defined by Strasburger. 'We speak of tropism when the organ takes up a resting position definitely *related to the effective stimulus*. Nastic movements, on the other hand, are curvatures which bring about a *particular position in relation to the plant*, and not to the direction of the stimulus.' [1]

In describing the direction of responsive movements, confusion is likely to arise unless the observer's point of view be carefully defined. An up-movement of the petal in a flower means approach towards the growing-point of the axis. This may be variously described as movement of closure or of folding. A down-movement may, on the other hand, be described as a movement of opening or of unfolding. If the movement be nastic, then the closure or the opening movement will remain the same, whether the organ be held in normal position or upside down. If, on the other hand, the direction of the movement be determined by the paratonic effect of an external stimulus, gravity for example, then the responsive movement in relation to the plant will be different. The closure-movement in the normal position will, on inversion, be reversed into a movement of opening. The reversal of closure into an opening movement or *vice versa* will thus be a test of the paratonic effect of geotropic stimulus.

Typical examples of thermonasty are afforded by the

[1] Strasburger, *Text-Book of Botany* (1912), p. 300.

flowers of *Crocus vernus* and *Tulipa Gesneriana*, spe[illegible] investigated by Pfeffer. He found that the flowers open[illegible] under the action of a rise of temperature, and closed under the action of a fall. He also established the important fact that the opening and closing of flowers is a phenomenon of differential growth under variation of temperature. The dorsiventral perianth-leaf of the flower is affected unequally at its two sides by rise or fall of temperature. In opening under rise of temperature, the upper side grows relatively the faster, the opposite effect being induced during fall of temperature. I shall show that thermonastic movements are not of one but of two distinct types: (1) the *positive*, in which, as in Crocus, rise of temperature induces a movement of opening; and (2) the *negative*, where rise of temperature induces a movement of closure, as in a number of the Water-Lilies (Nymphaea) which grow in India.

POSITIVE THERMONASTIC RESPONSE OF ZEPHYRANTHES

I first give an account of the movement of the petal of Zephyranthes, the reaction of which to variation of temperature is similar to that of Crocus. Viewed from above, the inner side of the petal of a flower is the upper side; under rise of temperature the flower opens evidently by the enhanced rate of growth of the relatively more active upper side, as shown by the following experiments.

Experiment 123. *Effect of variation of temperature.*—In obtaining a record, all the floral leaves except one were removed, this particular petal being attached to the recording lever. There was an up-movement, or a movement of closure, under fall of temperature, while rise of temperature induced a movement of opening. The up-movement [illegible] recorded by a down-curve and *vice versa* (fig. 124).

Experiment 124. *Responsive movement under* [illegible] I next determined the effect of radiation on the [illegible] of the petal. It has been shown that the effe[illegible] whether visible or invisible, are similar, t[illegible]

thermal rays being very pronounced. On subjecting the leaf to thermal radiation, the movement of response was one of closure (fig. 125), in sharp contrast with the movement of

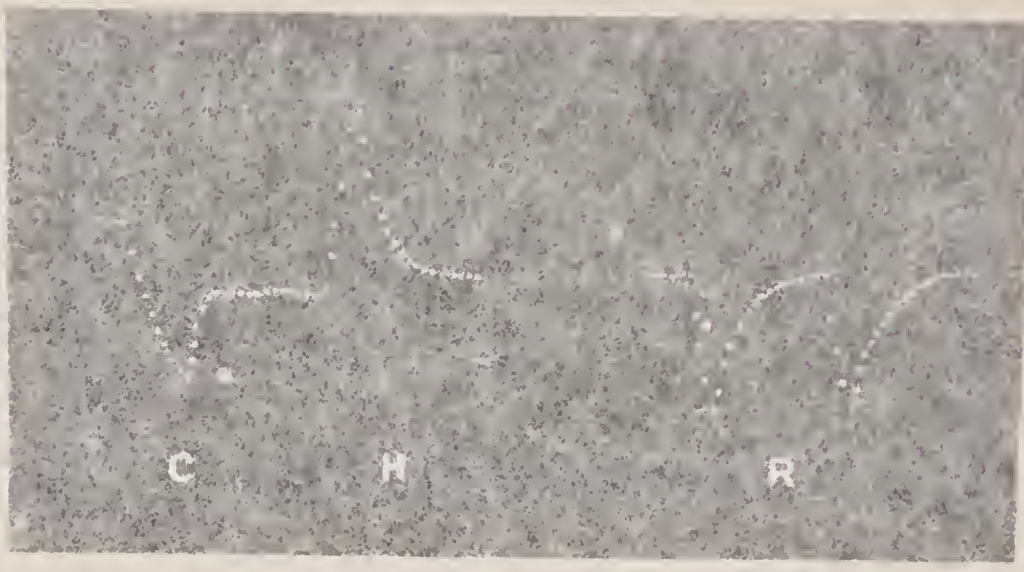


FIG. 124. FIG. 125.

FIG. 124. Thermonastic responses of petal of Zephyranthes. C, closing movement due to cooling; H, opening movement due to warming.

FIG. 125. R, closing movement due to heat-radiation. Note opposite responses to rise of temperature and to radiation.

opening under rise of temperature. These experiments clearly demonstrate the opposite effects of rise of temperature and of radiation.

The following is an example of *negative* thermonasty.

DIURNAL MOVEMENT OF NYMPHAEA

The Indian White Water-Lily remains closed during the greater part of the day and opens at night. Figs. 126 and 127 are photographic reproductions of the day and night positions of the flower.

The question arises whether the diurnal movements of the flower are predominantly tropic effects of photic or geotropic stimulation or are due to thermonasty.

Effect of recurrent light and darkness.—It has sometimes been supposed that the closure and opening of this flower are mainly due to the alternation of light and darkness.

But there are definite facts which do not by any means support this conclusion; for if the movements of the petals

FIG. 126. Nymphaea closed in daytime.

FIG. 127. Nymphaea open at night.

were entirely dependent on light, two opposite effects would be produced in the morning and evening respectively. But the Water-Lily is open at both these times. Moreover,

the course of the opening and closing movements is, as will presently be shown, not strictly coincident with the daily changes of light and darkness. The movement of the petals

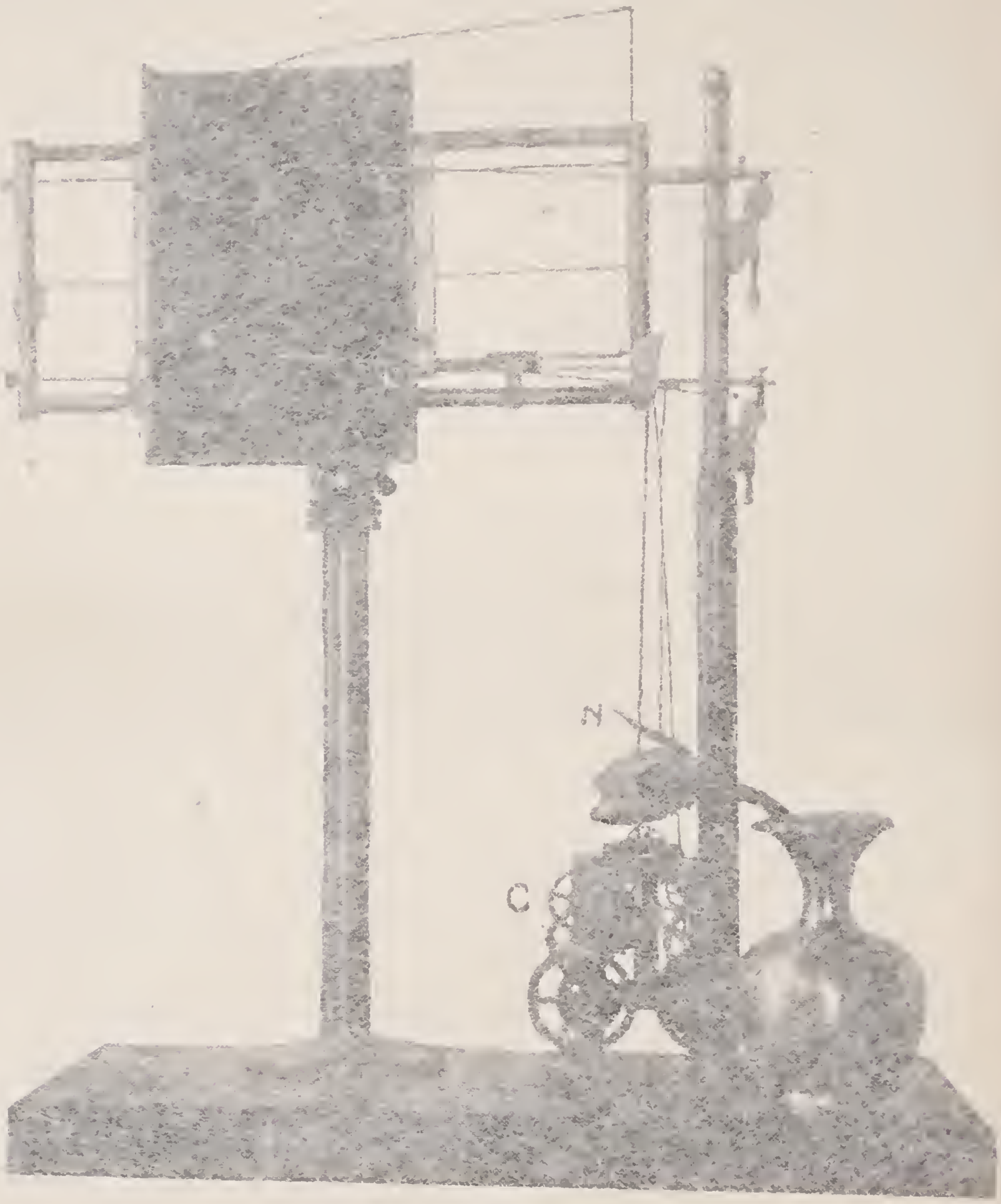


FIG. 128. The Thermonastic Recorder.

The specimen of Nymphaea has one of its perianth-leaves, N, attached to the short arm of the lower lever by a thread. T, metallic thermometer attached to the short arm of the upper lever; C, clockwork for oscillation of the plate.

of Nymphaea is therefore not essentially dependent on variation of illumination.

Possible effect of geotropism.—It may be asked, Does the stimulus of gravity exert any influence on the movement of the opening or closing of the flower? The petals close

up in the middle of the day, each of the petals standing erect. If the flower were susceptible to the stimulus of gravity, then, on turning the flower upside down, the closed petals in their inverted position would curl upwards and outwards, thus opening the flower. But no such effect takes place.

There remains only one other operative factor, namely, that of variation of temperature, the characteristic effect of which will next be demonstrated.

The Thermonastic Recorder

The apparatus is illustrated in fig. 128. One of the perianth-leaves, N, of the Lily is attached to the short arm of the lower recording lever. The metallic thermometer T is connected with the upper lever. Simultaneous records can thus be obtained of the diurnal variation of temperature and of the movement of the petal.

Experiment 125. *Effect of variation of temperature.*—Raising the temperature of the chamber in which the flower was placed induced a movement of closure shown by the down-curve (fig. 129).

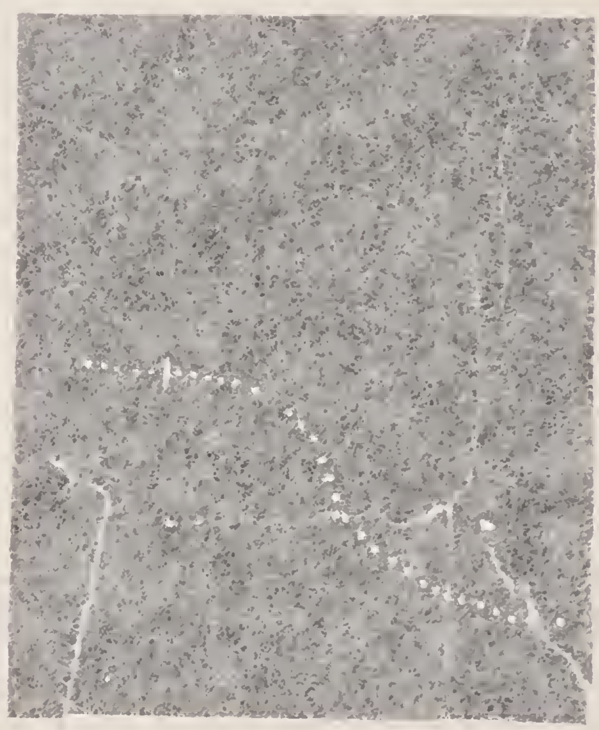


Fig. 129. Negative thermonastic response of Nymphaea

Application of heat at the vertical mark induced up-movement of closure seen as a down curve. Successive dots at intervals of a second.

The Diurnal Record

A continuous record of the movement of the petal was obtained from 6 P.M. to 12 noon next day. The flower was tightly closed from the forenoon, the perianth-leaves beginning to open out in the evening, at first slowly, then very rapidly; the flower became fully expanded by 10 P.M.

at night. Though the temperature continued to fall, there was no possibility of further expansion beyond the maximum. The temperature began to rise after passing through the minimum about 5 A.M., and the movement of closure set in with the rise of temperature till the flower became completely closed by 10 A.M. (fig. 130).

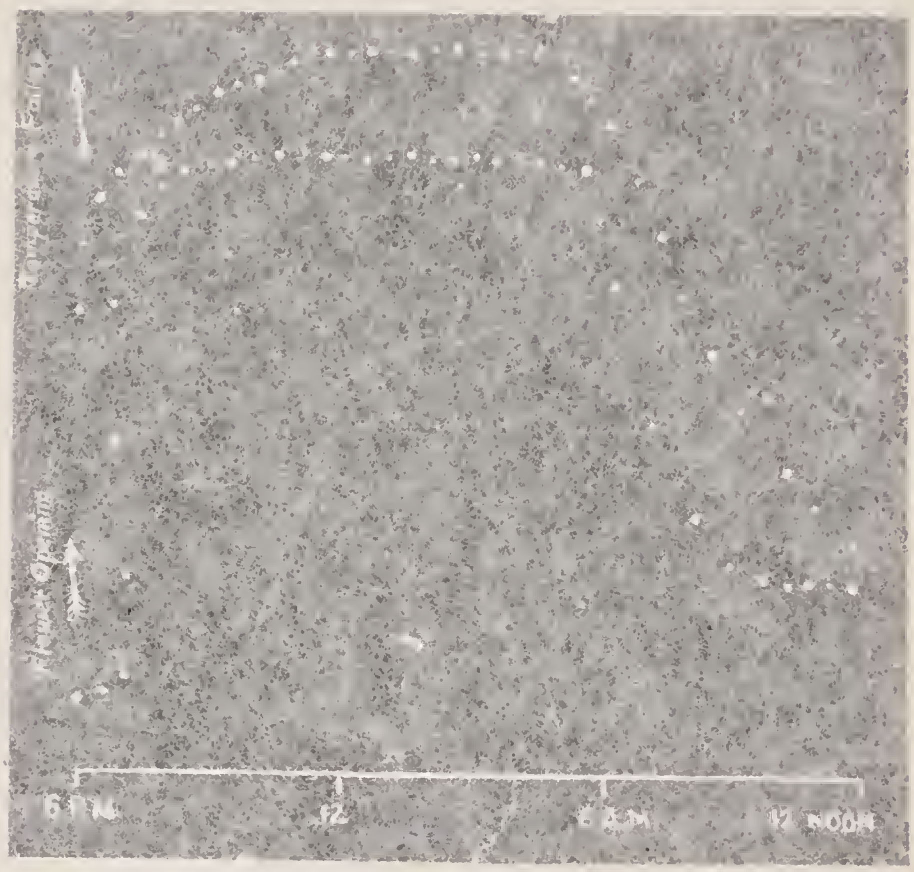


FIG. 130. Diurnal record of Nymphaea.

Upper record gives variation of temperature; the up-curve representing fall, and down-curve rise of temperature. The lower record exhibits the movement of the flower, up-curve representing the opening, and down-curve the closure of the flower.

The phenomenon of diurnal movement of the Water-Lily is therefore thermonastic, the floral leaves exhibiting a movement of opening at night owing to fall of temperature. The outer side is the more active.

The Water-Lilies of Europe close at night and open in the daytime. In searching for an Indian Water-Lily resembling the European type, I was successful in discovering a blue Lily, the diurnal record of which is exactly the opposite. In such cases it is the inner side that is relatively the more sensitive.

The results described lead to the following generalisation :—

1. Thermonastic movement occurs in organs which under variation of temperature, exhibit unequal growth of their two sides.

2. When the inner or upper side is the more active, rise of temperature induces a *positive* thermonastic movement, that is, the opening of the flower.

3. When the outer or lower side is the more active, rise of temperature induces *negative* thermonastic movement, shown by the closure of the flower.

The following tabular statement describes the different types of thermonastic organs.

TABLE XIX.—SHOWING THE EFFECT OF RISE OF TEMPERATURE ON THERMONASTIC MOVEMENT.

Type of reaction	Specimen
Positive, movement of opening	Zephyranthes Crocus European Nymphaea Indian blue variety of Nymphaea
Negative, movement of closure	Indian White Water-Lily

SUMMARY

Thermonastic movements are induced in growing anisotropic organs, the two sides of which exhibit different rates of growth under variation of temperature.

Rise of temperature induces greater enhancement of the rate of growth of the more active side; fall of temperature gives rise to the opposite effect.

Two types of thermonastic movements are met with, the *positive* exhibiting a movement of opening during rise of temperature; in these the inner side of the organ is relatively the more active. Examples of these are seen in Crocus, Zephyranthes, and in European and certain Indian Nymphaeas.

In the negative type, rise of temperature induces a movement of closure. Here the outer side of the organ is the more active. The Indian White Water-Lily belongs to this type.

CHAPTER XXI

THE DIURNAL MOVEMENT OF THE 'PRAYING' PALM

The report of the performances of the 'Praying' Palm of Faridpore drew my attention to this most remarkable phenomenon. This tree exhibited a regular up-and-down movement through a considerable extent day after day. It was a fully grown Date Palm (*Phoenix sylvestris*), the

FIG. 130. The 'Praying' Palm. The morning position.

length of the trunk being about 5 metres, with a diameter of 25 cm. It must have been displaced by a storm, so that the trunk was inclined to the vertical at about 60°. Fig. 131 shows the upper portion of the trunk. Two vertical stakes, each 1 metre in length, give the relative positions of the trunk in its two extreme excursions. In the course of its

daily movement, the trunk throughout its entire length was elevated in the morning and depressed towards the evening; the upper part of the rigid trunk was thus moved through the distance of 1 metre. The 'neck,' the upper end of the trunk bearing the leaves, was concave to the sky in the morning; in the afternoon the curvature disappeared

FIG. 132. The 'Praying' Palm. The afternoon position.

or was even slightly reversed. The large and long leaves, which pointed high towards the sky at the beginning of the day, were swung round towards the evening through a vertical distance of 5 metres (figs. 131, 132). To the popular imagination the tree appeared, at the time of evening prayer, to bend its neck and press its head of leaves against the ground in an attitude of devotion.

PHYSIOLOGICAL CAUSE OF THE MOVEMENT

What can be the underlying cause of this remarkable periodic movement? Is it due to mere physical expansion and contraction by heat or cold, or to some specific reaction of the living tree? If physical, the movement would still

rsist after the death of the tree; if physiological, the ovement would disappear.

The tree was old and died a natural death a year after e commencement of my investigations. I then received communication from the Government officer in charge of e district, that 'the palm tree is dead and its movements ve ceased.' This afforded conclusive evidence that the ovements had in some way been due to its vital activity.

The periodic movement of the tree must therefore be tributable to the physiological response of the living cells the diurnal changes of the environment—either the current alternation of light and darkness, or the diurnal anges of temperature. The only certain way of dis-riminating the effect of the one from that of the other was obtain a continuous record of the movement of the tree d find whether light or temperature maxima coincide th the maximal displacement of the tree.

The objects of the investigation resolved themselves nto the following:

1. A method of accurate and continuous record of the tree day and night for the determination of the exact times of maximum erection and of fall;
2. Comparative determination of the effects of diurnal variations of light and of temperature;
3. To ascertain whether the characteristic movement of the particular Palm was unique, or whether it was of more or less universal occurrence; and
4. Determination of the relatively more effective factors in the production of the diurnal movement.

The problem is complicated, the movement of the tree eing modified by so many factors. This was realised uring the course of my investigations on the subject, now xtending over twelve years. I will first describe the effects bserved under diverse experimental conditions, which have ed to the disentanglement of the individual effects of the veral factors in operation.

THE AUTOMATIC RECORDER FOR TREES

The record was obtained by the device illustrated fig. 133, for recording the diurnal movements of trees and

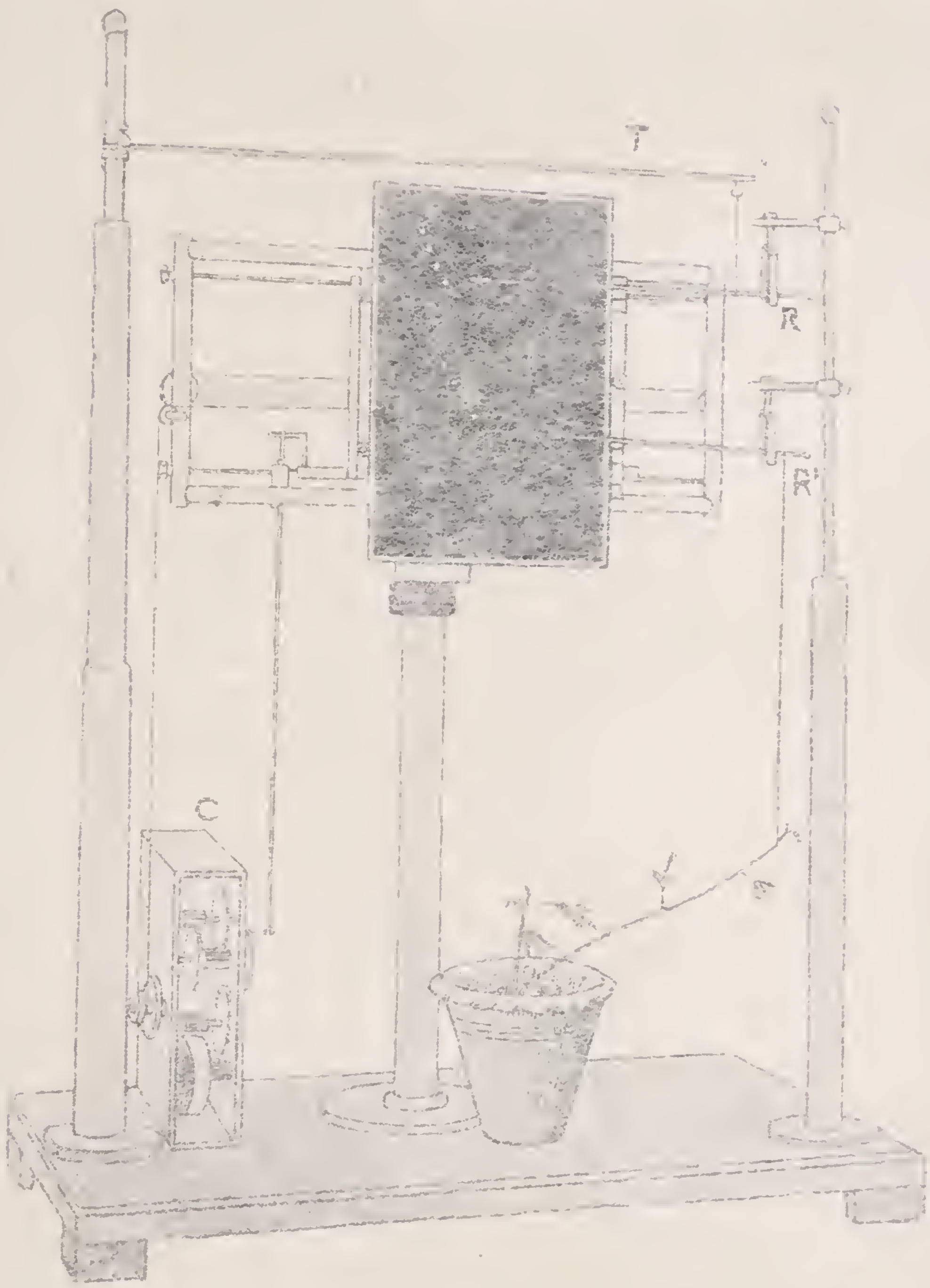


FIG. 133. Automatic Recorder of movements of trees and plants. T, differential metallic thermometer; R, recording lever for temperature; R', for recording plant-movement; C, clockwork for oscillation of recording plate. The same clockwork moves plate laterally for 24 hours.

other plants. One of the two writing levers gives the record of variation of temperature by the Thermograph, and the other lever records the up or down movement of the tree throughout 24 hours. As the extent of the

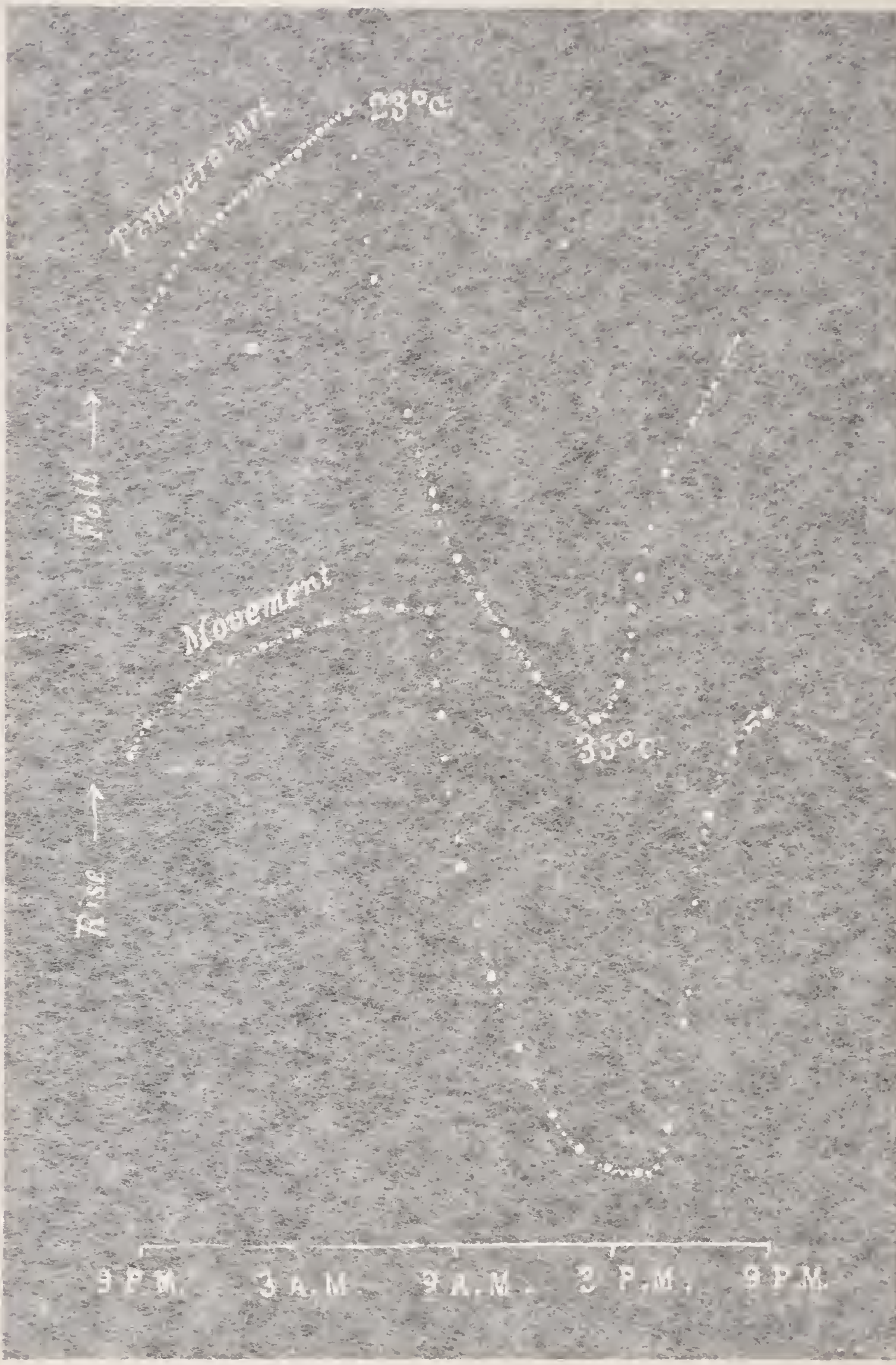


FIG. 134. Record of diurnal movement of the 'Praying' Palm (Phoenix sylvestris).

Thermographic curve for 24 hours commencing at 9 in the evening, is given in the upper record in which the fall of temperature is represented by an up-curve. The corresponding diurnal curve of movement of the tree is given in the lower. Successive dots at intervals of 15 minutes; thick dots, intervals of an hour.

movement of the tree was considerable, means had to be employed for the reduction of the movement recorded by the lower writing lever. On the oscillating plate successive dots were made at intervals of 15 minutes, the thicker dots being inscribed at intervals of an hour. The erectile movement of the tree is represented as an up-curve, while rise of temperature is recorded as a down-curve.

The Diurnal Record of the Tree

Experiment 126.—Hasty observation led people to believe that the tree lifted itself at sunrise and prostrated itself at sunset; but the continuous record obtained with my apparatus proved that the tree was never at rest, but in a state of continuous movement which underwent periodic reversal (fig. 134). The tree attained its maximum erection at 7 in the morning, after which there was a rapid fall. The downward movement reached its maximum at 3.15 P.M., after which it began to lift itself very slowly, then more rapidly, until it lifted itself to the highest position at 7 next morning. This diurnal periodicity was maintained day after day. *The movement was by no means passive, but was effected with an active force sufficient to lift a man off the ground.*

The next point is the determination of the relative effects of variations of light and of temperature in inducing the diurnal movement.

The Relative Effect of Light

The following considerations will help in deciding whether or not light had any perceptible influence in the production of the periodic movement of the tree.

1. Since the movement has been shown to be a physiological phenomenon, the stimulus of light, in order to be effective, must act directly on the living tissue. In the case of the Palm this is impossible, for the bark of the tree is of considerable thickness, and the thick bases of dead

leaves completely screen the deep-lying living tissue light.

2. The curve of the movement of the tree affords, ever, data for correct inference as to the possible effe light. If the action of light is determined by its maxi intensity, then there should be a climax at noon, and opposite at midnight. But the highest erection was re not at noon, but at 7 in the morning; the lowest fall, on other hand, was attained not at midnight, but in the a noon. Again, if the movement was caused by the cum tive action of light, then the maximum extent of moven either up or down, should be attained shortly before even but this was not the case, for it occurred several h earlier, at about 3 P.M.

It is thus probable that light had very little influe on the movement of the tree. I will describe additi experiments in support of this conclusion.

Effect of Variation of Temperature

Turning next to the factor of thermal change, the record shows that the curve of the movement of the tree is practically a replica of the curve of variation of temperature (*see* fig. 134). The rise of the tree followed the fall of the temperature and *vice versa*. A lag will be noticed at the turning-points of the movement; thus, while temperature began to rise at about 6 A.M., the tree did not begin to fall till an hour afterwards. Again the turning-point from rise to fall of temperature was after 2.45 P.M.; the downward movement of the tree was, however, not reversed into one of erection till after 3.15 P.M., the lag being about 30 minutes. The delay is attributable to two causes: it took some time for the thick trunk of the tree to attain the temperature of its surroundings; in addition to this, physiological inertia delayed the reaction.

In reference to the incidence of *thermal noon*, already defined in the last chapter, it is modified (1) by the season:

(2) by the locality, whether it is exposed or shaded; (3) by the condition of the weather; and (4) by the radiation of heat from the ground. It varies according to circumstances from 1 to 3 P.M. The *thermal dawn*, generally speaking, is shortly after sunrise. The movement of the tree lagged somewhat behind the change of temperature; erection commenced after the thermal noon, and the fall began after the thermal dawn.

The Periodic Movement of Sijbaria Palm

Another question which had to be investigated was whether the movement of the Faridpore Palm was a unique phenomenon, or whether other Date Palms exhibited similar movements. With this end in view, I experimented with a Date Palm that was growing at my Research Station at Sijbaria on the Ganges, situated at a distance of 200 miles from Faridpore.

Experiment 127.—The surrounding conditions were very different; the tree itself was much younger and was at an inclination of 20° to the vertical instead of 60° as in the previous case. The tree was enclosed in a dark tent to exclude the action of light. The diurnal curve of its movement was found to be very similar to that of the Faridpore Palm, though the extent of its movement was considerably less. The tree attained its highest erect position at 7.15 A.M. and the lowest at 3.45 P.M. (fig. 135). In settled weather the diurnal rise and fall of temperature is very regular, and so was the movement of the tree. But under less settled conditions, owing to change of direction of wind, the temperature curve exhibited fluctuation. It was a matter of surprise that the plant-record should have repeated this fluctuation with astonishing fidelity, as seen in the common twitch in the two curves shortly after 8 A.M. There can, therefore, be no doubt whatever about the movement being principally due to variation of temperature.

The extent of the up and down movement of the Sijbaria

Palm was very much less than that of the Faridpore, presumably because its angle of inclination to the vertical was very much smaller, and the tree was therefore less effectively subjected to the stimulus of gravity.

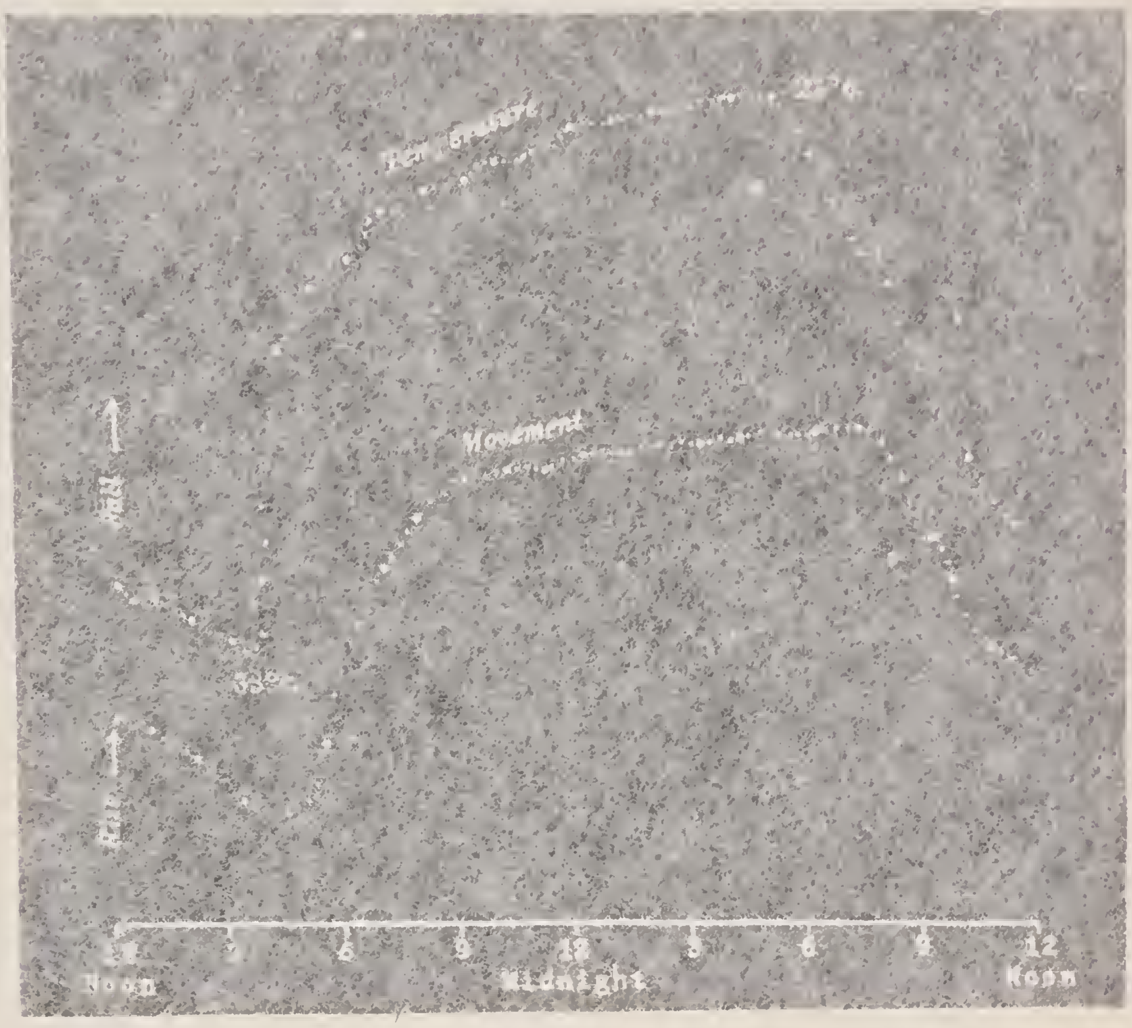


FIG. 135. Record of the Sijbaria Palm from noon for 24 hours. Successive dots at intervals of 15 minutes.

It will be shown in the next chapter that a unidirectional movement cannot take place under diffuse stimulation which acts on all sides of an organ, unless it has been rendered anisotropic. There are reasons to believe that the stimulus of gravity is effective in inducing anisotropy.

The next question is—Is the diurnal movement confined only to the Date Palm or do other Palms exhibit similar movements?

DIURNAL MOVEMENT OF KENTIA PALM

In answer to this question I planted in the grounds of my Institute a Kentia Palm at a considerable inclination

to the vertical. After a time it became curved upwards under the stimulus of gravity, and showed a very marked up and down movement similar to that of the Faridpore

FIG. 136. The Diurnal Indicator.

Movement up and down of tree indicated by anti clockwise or clockwise movement of index on the circular scale (Kentia). (*See* text.)

Palm. The apparatus described below made it easy to demonstrate the periodic diurnal movement.

The Diurnal Indicator.—A small wheel is adequately supported in a fork not shown in the figure. The upper end of a string S is attached to the Palm where it curves up,

the string itself making a loop round the wheel, the low
end of the string being tied to the spiral spring T. Wh
the tree is erecting itself, the wheel is rotated anti-clockw
the angle of rotation being read by the index on a circu
scale C. Fall of the tree causes clockwise rotation of th
wheel (fig. 136). By making the diameter of the wh
sufficiently small the Diurnal Indicator can be m
extremely sensitive.

From the results that have been obtained it wo
appear that two conditions are necessary to ensure
striking display of the periodic up and down movemen
the tree. The first is that the tree should have been rend
anisotropic by the previous action of the stimulus of gra
the second is that the tree should be subjected to the diu
variation of temperature. These, as well as other con
tions affecting the diurnal movement of plants, will
treated in detail in the next chapter.

SUMMARY

The 'Praying' Palm of Faridpore, growing at an incli
tion of 60° to the vertical, exhibited a diurnal movement su
that its head became erected in the morning and lower
towards the evening, the outspread leaves becoming press
against the ground.

Diurnal records of temperature and of movement of th
tree show that the two curves closely resemble each other
The rise of temperature was followed by the fall of the tr
and *vice versa*.

The movement was not physical but physiological,
was proved by cessation of all movement after the death
the tree.

The influence of light is negligible in the diurnal mov
ment.

The movement is found to be essentially due to t
diurnal variation of temperature, a slight fluctuation

temperature being often quickly followed by a corresponding movement of the tree.

Anisotropy induced by previous geotropic stimulation appears to be a contributory factor in the striking manifestation of diurnal movement. For it appears that the greater the inclination of the tree to the vertical, the greater is the extent of its periodic movement under variation of temperature.

CHAPTER XXII

DIURNAL MOVEMENTS OF PLANTS RENDERED ANISOTROPIC BY GRAVITY

FACTS were given in the previous chapter which seem to indicate that one of the factors in the diurnal movement

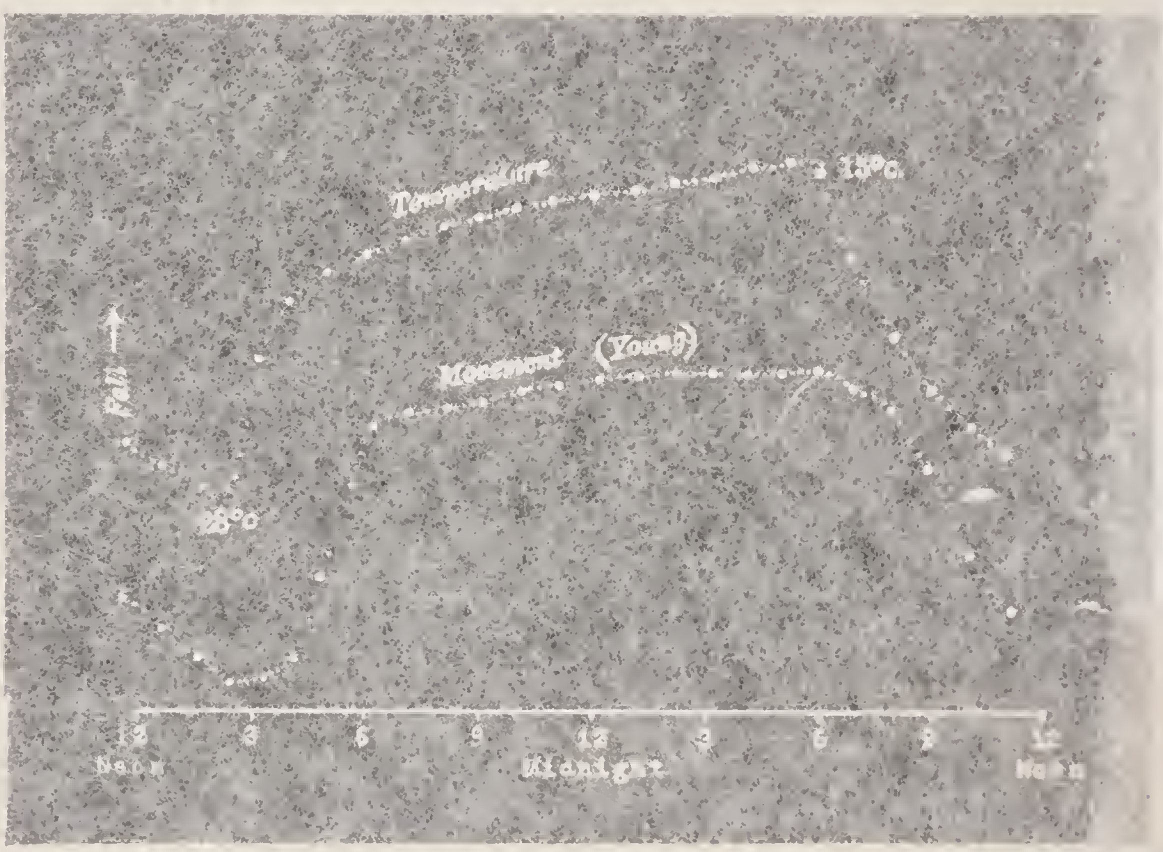


FIG. 137. Diurnal curve of movement of procumbent young of Mimosa pudica.

Successive dots at intervals of 15 minutes.

of the Palm under variation of temperature is the previous induction of anisotropy by the stimulus of gravity. The question next arises whether these movements

characteristic only of Palms, or whether they can also be detected in other plants under parallel conditions. In answer to this, I first experimented with the procumbent stem of a young plant of Mimosa (fig. 137).

Diurnal Movement of Stem of Mimosa

Experiment 128.—The stem was nearly horizontal and therefore subjected to the stimulus of gravity. The diurnal records of the movement of the stem and of the variation of temperature showed that while the temperature rose from noon to 2.30 P.M., the Mimosa stem exhibited a fall. The temperature fell after the thermal noon, this being attended by rise of the stem, the lag of response being about an hour. The erectile movement continued with the fall of temperature till about 6 next morning. After this the temperature began to rise and the stem responded by a fall. As in all cases hitherto considered, the erectile movement of the plant occurred from thermal noon to thermal dawn, the fall taking place from thermal dawn to thermal noon (fig. 137). The diurnal record of the procumbent stem of Mimosa is thus in every way similar to that of the Sijbaria Palm Tree.

If it be true that induction of anisotropy by the geotropic stimulus renders the stem of the Palm effective to respond to variation of temperature by the characteristic up and down movement, then ordinary stems curved under the action of gravity, as well as dia-geotropically outspread leaves of plants, might also be expected to exhibit such movements.

Diurnal Records of Stem and Leaf

Experiment 129.—I took diurnal records of a geotropically curved stem of Tropaeolum and of a dia-geotropic leaf of Dahlia for two days in succession. The thermal record shows the usual fall of temperature after thermal noon, from

2.45 P.M. to thermal dawn next morning at 6 A.M., that is to say, for nearly 16 hours. Rise of temperature occurred through the same range in about 8 hours. The average

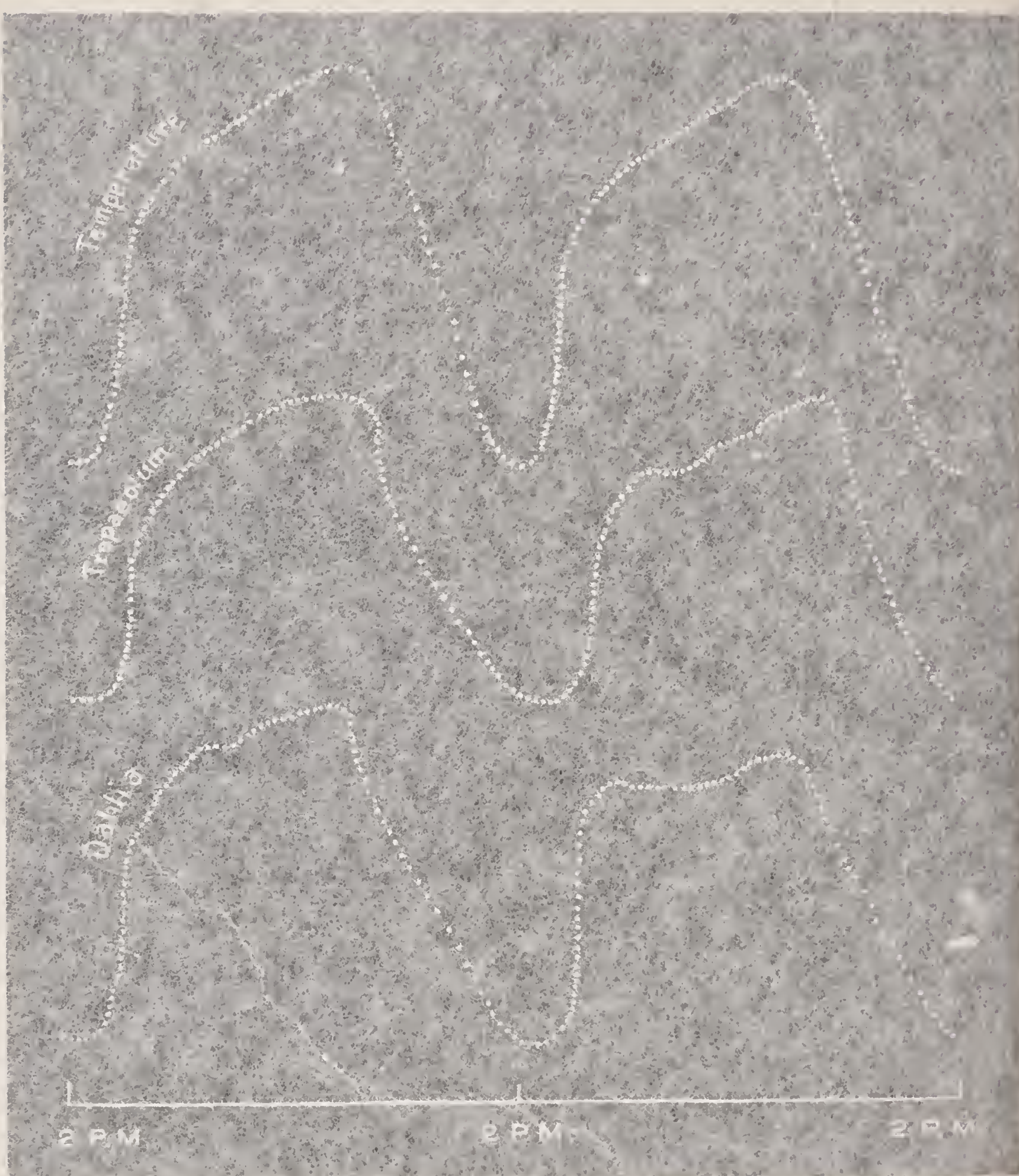


FIG. 138. Diurnal curve of the procumbent stem of Tropaeolum majus and of the leaf of Dahlia for two successive days. In the thermographic record the up-curve represents fall and down-curve rise of temperature.

rate of rise of temperature was thus about twice as quick as the average fall, very clearly shown by the difference in the slopes of the curve during thermal descent and ascent.

The records of the movements of the procumbent stem and leaf exhibited a striking parallelism. They became erected from thermal noon to thermal dawn, and underwent a fall from thermal dawn to thermal noon. The descent of the curve is, as also that of the thermal curve, relatively more abrupt. The records on two successive days are seen to be very similar (fig. 138).

Diurnal Record of Tropaeolum under Constant Temperature

The fact that the diurnal movement was due to variation of temperature was further proved by maintaining the Tropaeolum stem, employed in the last experiment, at a constant temperature.

This was secured by the construction of a special chamber, in which the plant and the recording apparatus were placed. This chamber was maintained at a constant temperature by an electro-thermic regulator which interrupts the heating current as soon as the temperature of the chamber is raised a hundredth part of a degree above the predetermined constant temperature. The automatic make-and-break of the current takes place in rapid succession, so that the temperature of the chamber is maintained constant within one tenth of a degree Centigrade, throughout day and night.

Experiment 130.—The records of the Thermograph and of the plant's movements were now taken simultaneously. On the first day the temperature was maintained constant, with the result of abolition of the periodic movement of the plant. This is clearly seen from the horizontal curves recorded during the first 24 hours. The thermal regulator was then put out of operation, thus restoring the normal diurnal variation of temperature; the result of this was that the stem exhibited once more its normal periodic movement (fig. 139).

Experiment 131.—The diurnal records of adult leaves of a number of plants, such as Dahlia, Papaya, Croton and others, exhibit the same characteristics as shown by the Palms and by the geotropically curved stems. In all these, the fall of temperature from thermal noon to thermal dawn

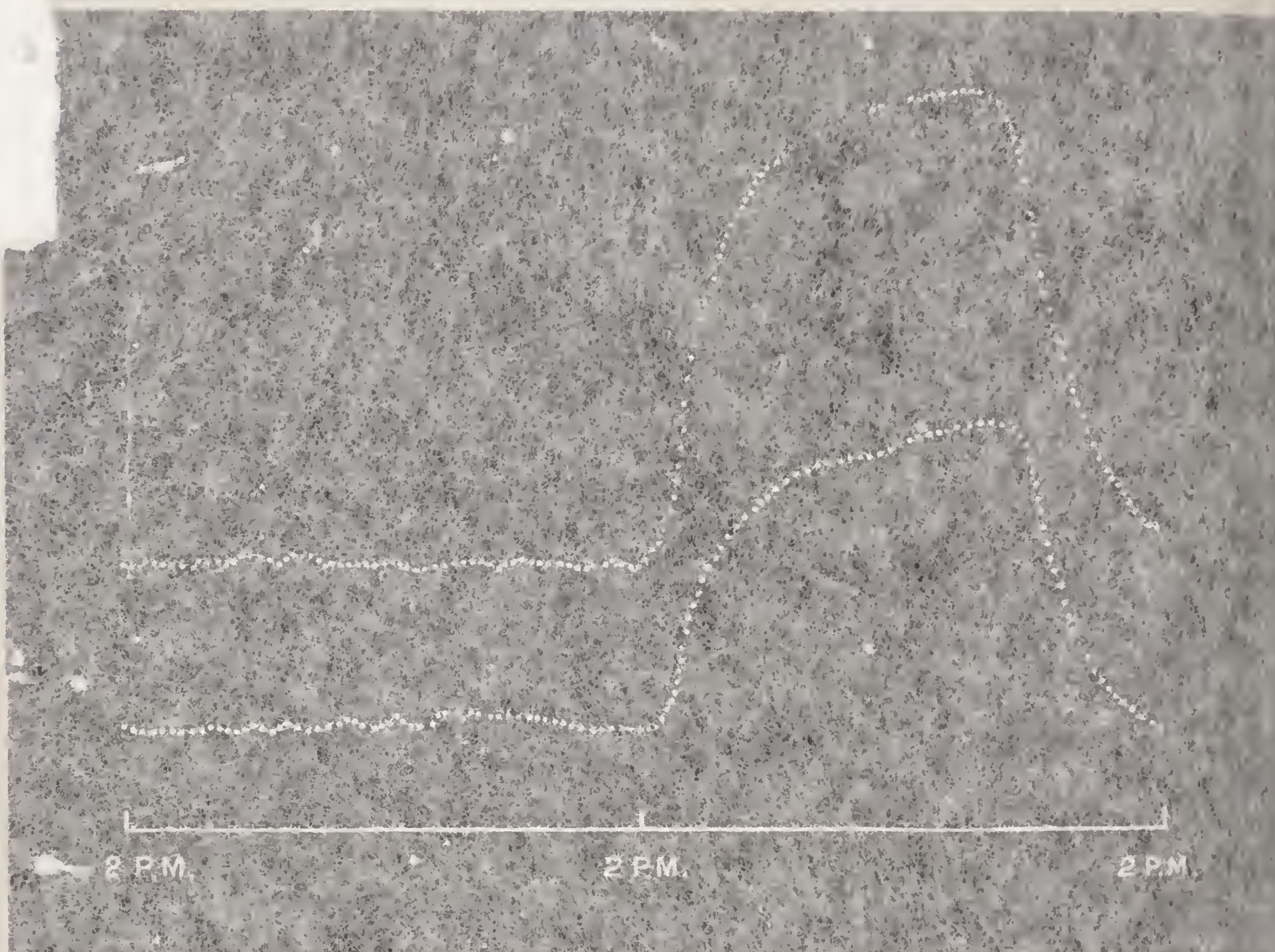


FIG. 139. Abolition of diurnal movement in Tropaeolum under constant temperature, and its restoration under normal daily variation. The upper record is of temperature and the lower of plant-movement. The horizontal parts of the record relate to the period of constant temperature.

induced an up-movement of the leaf, while rise of temperature from thermal dawn to thermal noon caused a fall (fig. 140). There is an individuality which characterises the record of each species of plant, and thus makes it possible to identify it from its autograph.

The facts given above appear to indicate that organs previously subjected to gravitational stimulation exhibit characteristic diurnal movements under variation of tem-

perature. The possibility of the influence of other factors in the diurnal movement will now be considered.

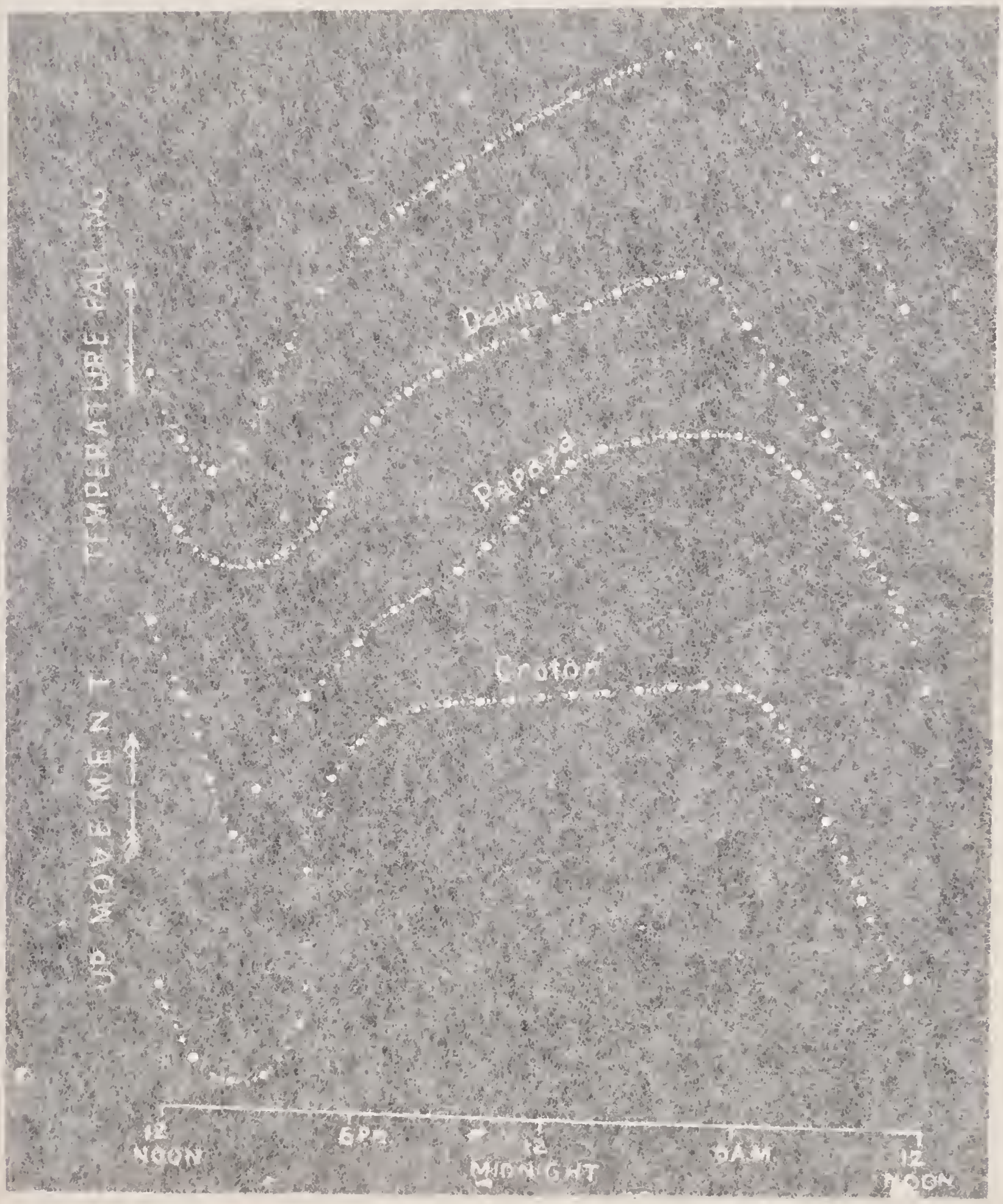


FIG. 14?. Diurnal record of adult leaves of Dahlia, Papaya and Croton.

DIURNAL VARIATION OF TENSION AND BULK IN DIFFERENT ORGANS

Kraus found that the tissue-tension of a shoot exhibits a daily periodicity under normal alternation of day and night. The tension diminishes throughout the day as the

intensity of light increases, while it decreases in the early afternoon as the intensity of light diminishes. Variation of temperature within normal limits does not, according to him, appear materially to affect the daily period. In other words, it is the variation of light, and not of temperature that has a marked influence on the tension of the tissues. In the case of diurnal movement of trees, however, the effective factor is *not* light but variation of temperature.

Even if variation of tension were due to variation of temperature, it is by no means clear how this could cause a definite up and down movement of the tree. Rise or fall of temperature acting on the tree as a whole cannot produce any unidirectioned movement unless one side is relatively more active than the other, as is the case only in anisotropic organs.

In a young tree the geotropic effect is outwardly manifested by the upward curvature induced in the growing region. I have shown further that the cortex of an old rigid stem, though incapable of outward movement, is still sensitive to stimulus.[1] The cortex of the tree throughout its length may thus be rendered differentially excitable by the prolonged action of geotropic stimulus which renders it anisotropic. The fact that a condition of anisotropy is essential for the production of diurnal movement under diffuse stimulation will presently be demonstrated.

Diurnal Variation of Tissue-tension in Mimosa

It has just been stated that the characteristic response under variation of temperature is best exhibited by an organ which is anisotropic. Millardet found a daily periodicity of tension in *Mimosa pudica*, shown by the up and down movements of the leaf; the organ of response is here the pronouncedly anisotropic pulvinus. Millardet was thus able to correlate the periodic movements of the leaf with variation of temperature and of tension. The maximum

[1] *The Motor Mechanism of Plants* (1928), p. 141.

tension was found to occur before dawn, when the petiole was erected towards the apex of the stem. Tension decreased during the day and reached minimum early in the evening, when the petiole fell, the movement being away from the apex of the stem. The relation between change of temperature and tension increased with the rise and decreased with the fall of temperature.

The anisotropy of the responding pulvinus in Mimosa is natural and permanent. This suggests the question, What would follow if the Mimosa plant were placed upside down? The periodic movements of the petiole in relation to the axis of the plant will obviously remain the same, but will appear reversed in space. Maximum tension in the morning will make the petiole approach the tip of the stem—that is to say, the movement will be downwards, instead of upwards as in the normal position.

Effect of Reversal of Induced Anisotropy on Diurnal Movement

The next case to be considered is that in which the anisotropy is not natural or permanent, but has been induced by geotropic stimulation and is thus capable of becoming reversed under appropriate conditions. For example, if a stem, say, of Tropaeolum be held horizontal, it will curve upwards; one side, the upper (A), will be contracted, and the lower (B) expanded, the radial organ thus becoming anisotropic. Next, if the stem be inverted by rotating it through 180°, then the side A will have become the lower; the former geotropic curvature will shortly become reversed, and A will undergo a change from contraction to expansion. The induced anisotropy will thus undergo reversal.

If the periodic movement depends on the anisotropy that is induced by geotropic stimulation, three stag[illegible] transformation should be presented in the diurnal re[illegible] of the plant.

1. The stage of normal anisotropy, when A is th[e] upper side and contracted ;
2. The transitional, shortly after inversion (A below), and
3. The stage of reversed anisotropy, when the plant i[s] geotropically readjusted in the new position (A below and expanded).

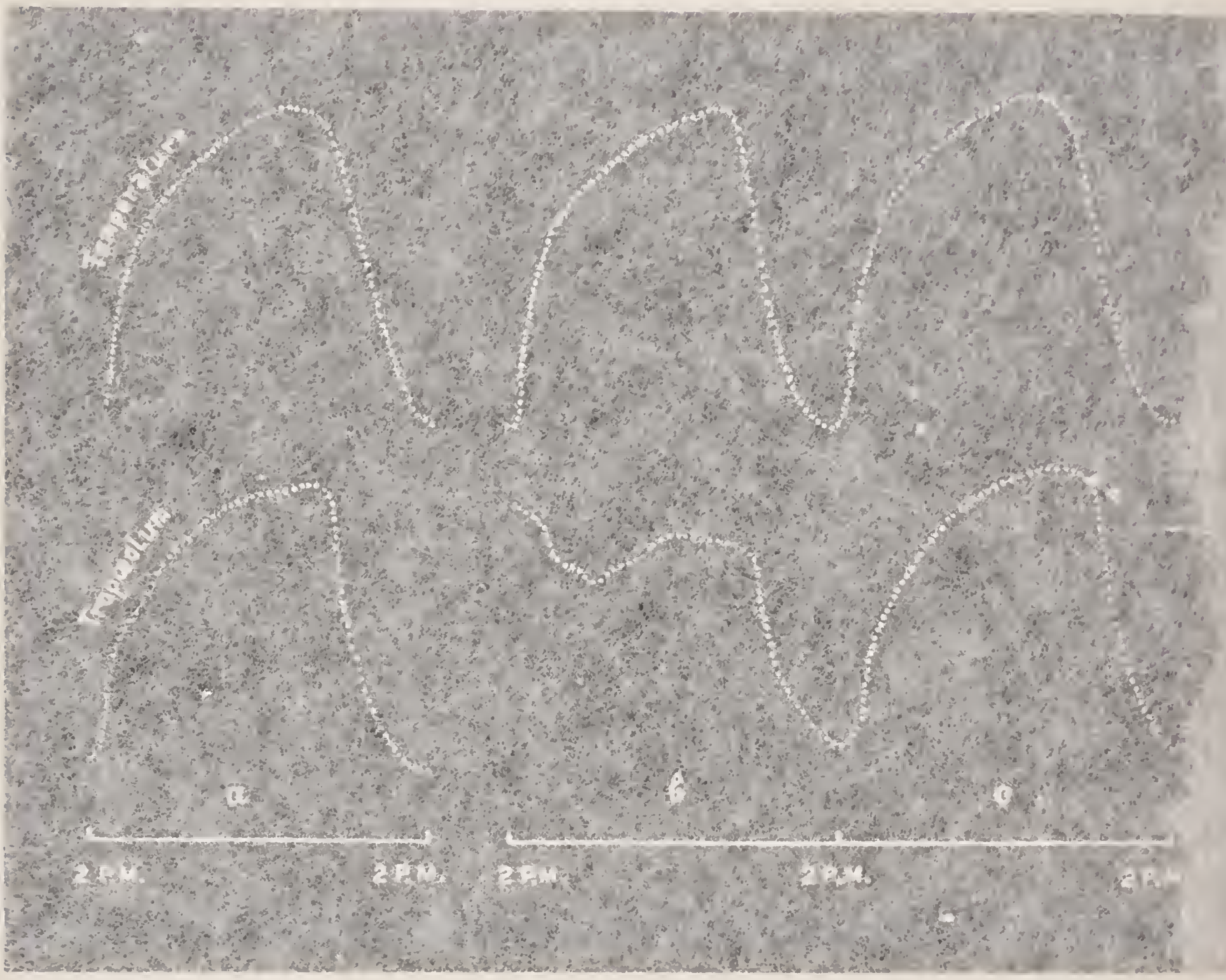


FIG. 141. Effect of inversion of the plant on diurnal movement. *a*, normal record; *b*, record 24 hours after inversion, and *c*, after 48 hours. (Tropaeolum.)

Experiment 132.—The normal, the transitional and th[e] reversed diurnal records were obtained with an identica[l] horizontal stem of Tropaeolum subjected to stimulus o[f] gravity (fig. 141). In *a* is seen the normal diurnal curv[e] when the surface A was uppermost ; the specimen wa[s] ...inverted, and it took nearly two days for the stem t[o] ...just itself to the new state of geotropic equilibrium. ...ecord *b* was recommenced 24 hours after inversion; ...rsistence of the previous movement is seen in the ...l curve during the first half of this record ; but in

the second half the record became true; on the third day the inverted plant gave a record (*c*) which from an external point of view was similar to that given by the plant in the first or normal position.

There is another aspect of the subject which may be of interest, namely, whether geotropic irritability itself undergoes variation under high temperatures in the tropics. The results of various investigations have shown (as will be described in a later chapter) that geotropic stimulation is effected by the fall of starch-grains in the cells of the statolithic apparatus. Is the efficiency of this apparatus modified by high temperature? This problem I investigated by the method of geo-electric response, in which the excitatory reaction under geotropic stimulation was detected by the concomitant electric response. I found, for example, that while the intensity of geo-electric response was, generally speaking, very marked in Calcutta during the month of February with an average temperature of 20° C., it disappeared by the middle of April, when the average temperature had risen to about 30° C. With *Tropaeolum majus* I could get no response even in March. On repeating the experiments with the same plant three months later at my Mayapuri Research Station, Darjeeling, I was considerably surprised to find that the geo-electric response of Tropaeolum was fully vigorous at the hill station, where the temperature was lower than 20° C. This would appear to show that geotropic irritability is accentuated within limits by a fall of temperature and depressed by a rise. Though some plants exhibit this change in a marked degree, yet it cannot be asserted that all plants exhibit it. The particular periodic movements under consideration can, however, be explained by the effect of variation of temperature on an organ rendered anisotropic by geotropic stimulation.

Analogy with Thermonasty

It has been shown that in an anisotropic growing organ ... of temperature, acting on it as a whole, induces a

thermonastic movement in one direction, while fall of temperature causes movement in the opposite direction. In many ways the movement of the Palm appeared to be thermonastic. Thermonasty has, however, been defined as the characteristic of differentially *growing* organs the anisotropy of which is natural and ingrained. But since I have shown (1) that there is a continuity of reaction between growing and non-growing organs, and (2) that anisotropy may be induced in an organ by the prolonged action of geotropic stimulus, it follows that the phenomena of the diurnal movements of trees and other organs may well be included under the wider generalisation of Thermonasty.

It will be convenient to use the short term *thermo-geotropism* as a descriptive phrase for the diurnal movements under variation of temperature of plants rendered anisotropic by geotropic stimulation.

Effect of Transpiration on Periodic Movement

A tree laid horizontally would exhibit a passive downward droop due to loss of turgor, resulting from excessive transpiration, this loss being very great at midday; at night there might be an opposite movement on account of diminished transpiration. But such movements, more or less passive, would not account for the active force which enabled the Faridpore Palm to lift a man off the ground (p. 229). An additional factor, not entirely dependent on transpiration, thus appears to co-operate in the diurnal movement. Whether this is so or not is demonstrated by the following experiments.

Experiment 133. *Periodic movement after abolition of transpiration.*—A Kentia Palm was placed horizontally in my greenhouse under a canvas tent in semi-darkness; the tent also protected the plant from mechanical disturbance caused by gusts of air. After taking these precautions it was easy to obtain very accurate records of the diurnal movement of the Palm by means of the Automatic Rec

The record was taken on the first day under normal transpiration (middle record, fig. 142). On the second day the

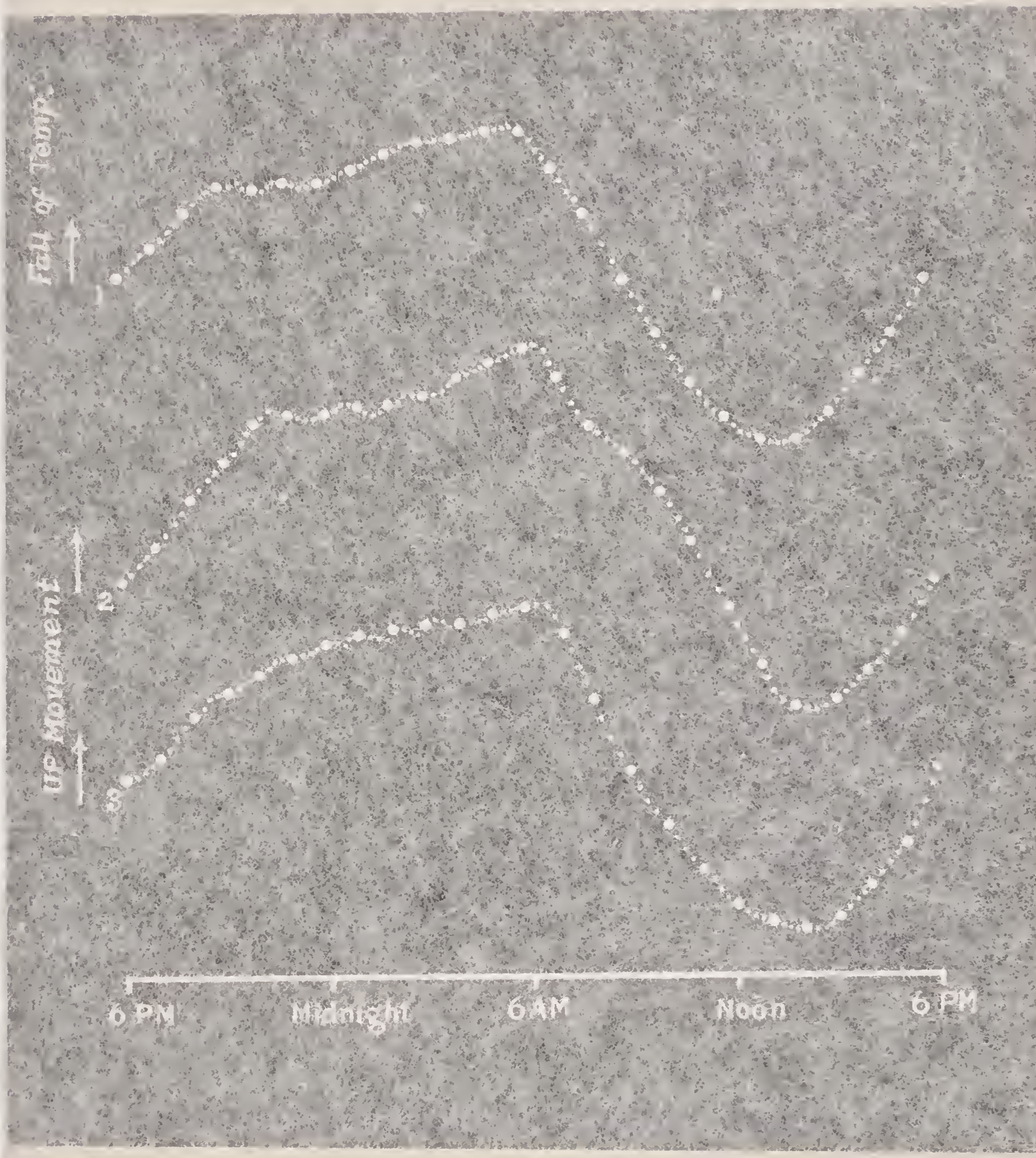


FIG. 142. Record of Kentia Palm before and after abolition of transpiration.

1. Record of diurnal variation of temperature, which was very similar on two successive days.
2. Diurnal record of the Palm under normal transpiration.
3. Persistence of diurnal movement after abolition of transpiration. (*See* text.)

stem and all the leaves of the Palm were very thickly covered with an impermeable coating of vaseline, which practically

abolished the loss of water by transpiration. Any periodic movement due to change in the rate of transpiration must now have come to an end. The record (lowest illustration, fig. 143) shows that there was no such arrest of movement;

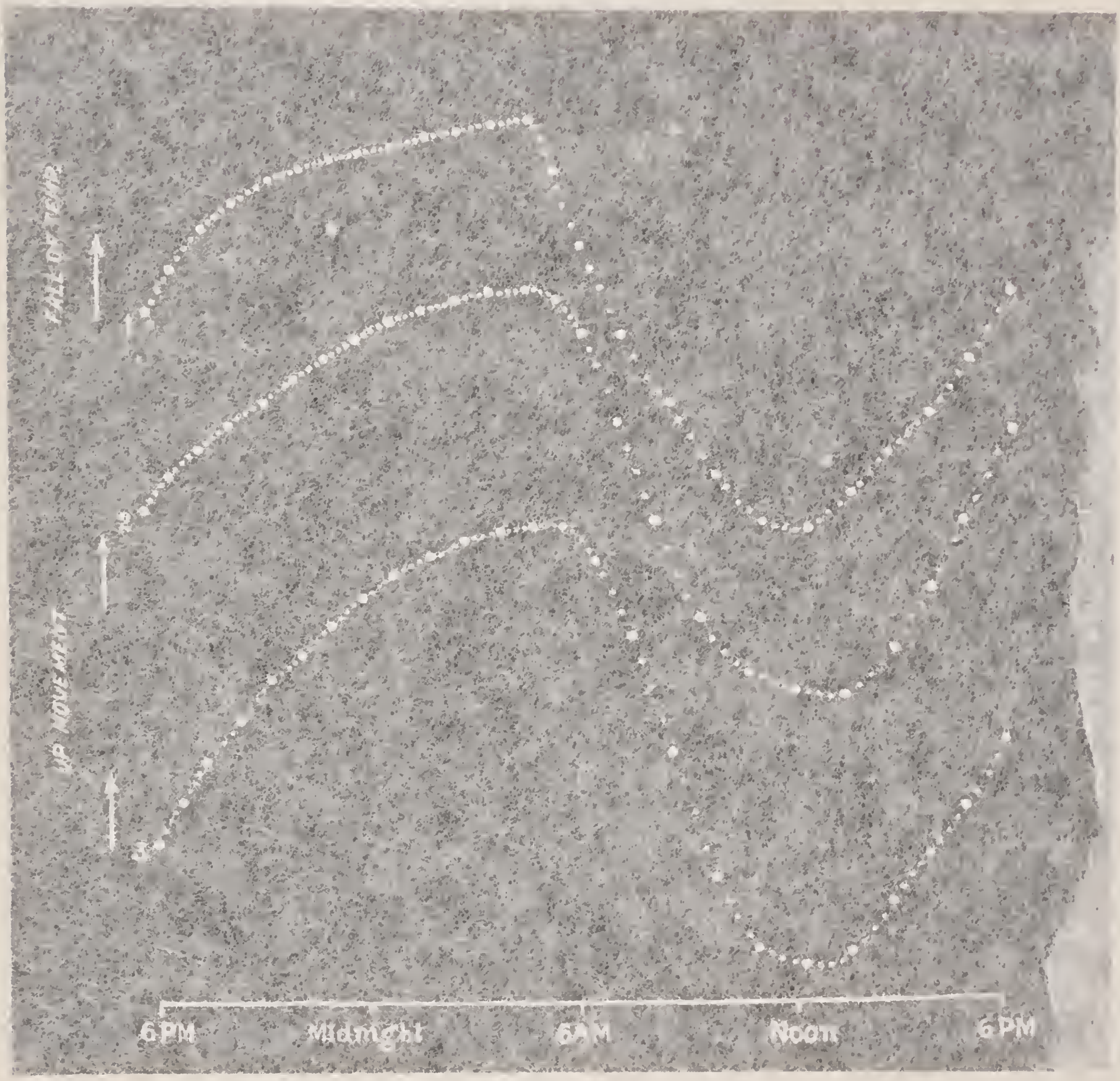


FIG. 143. Parallel record of a dia-geotropic leaf (Erythrina indica)

1. Record of diurnal variation of temperature.
2. Normal record of diurnal movement.
3. Diurnal record of movement after abolition of transpiration.

the vaselined tree executed the diurnal movement in much the same way as under normal conditions; and not only on that day but even on the next day as well.

Experiment 134. *Periodic movement of leaf after abolition of transpiration.*—A parallel experiment was carried out with the dia-geotropic leaf of *Erythrina indica* (fig. 143). The results are [illegible] th the [illegible]

Keutia Palm. Record 1 is of diurnal variation of ure; record 2 is the normal diurnal record of ment of the leaf; record 3 was taken of the after the plant and all its leaves had been thickly ith vaseline. The abolition of transpiration is ave had little effect on its diurnal movement.

facts described afford conclusive evidence that the movement is not mainly dependent on changes ispiration: that there is another factor, defined rmo-geotropism, which co-operates in the diurnal ents of plants.

SUMMARY

itinuity is shown to exist between the thermo-pic response of rigid trees, young stems, and adult of plants.

ll these an erectile movement is exhibited from noon to thermal dawn, and a movement of fall ermal dawn to thermal noon.

predominant effect of variation of temperature on irnal movement is demonstrated by the absence of iovement when the temperature is constant.

ie effect of the stimulus of gravity in inducing aniso-, which determines the characteristic diurnal move-, is proved by the effect of inversion of the plant on liurnal record.

he activity of thermo-geotropism as an independent or in the diurnal movement appears from its persist-e after the abolition of transpiration.

The thermo-geotropic movement is in many ways logous to the thermonastic movement. A wider eralisation is reached by the inclusion under the head of rmonasty of the response of non-growing organs rendered otropic by the stimulus of gravity.

CHAPTER XXIII

PHOTOTROPIC TORSION

IN addition to positive or negative curvature ind light, a torsional response also occurs under cer ditions. A leaf when struck laterally by light u a twist, so that the upper surface is placed more right angles to the incident rays. It has been that such torsions were produced by the action of of external factors, such as light, gravity, and weig organ, which individually led to curvature but combination induced torsion. Later investigatio however, shown that torsion actually occurs wh alone is the external factor. No satisfactory exp has, however, been given of the mechanics of the movement.

The experiments here described were planned to light on this obscure phenomenon. They show :

1. That the torsional response is not dependent combination of two curvatures ;
2. That it is independent of the effect of weight
3. That it can be induced not merely by the of light, but by all forms of stimulation ;
4. That the direction of the torsional response d on two factors: the direction of the incident sti and the differential excitability of the orga
5. That there is a definite law which determi direction of the responsive movement of to

Experimental Arrangements

I will first describe a typical experiment on torsional response under the action of light. It has been shown, in the case of the pulvinus of Mimosa, that light of moderate intensity and of short duration applied on the upper half induces a slow up-movement, while the stimulus of light applied below induces a more rapid down-movement. The difference is due to the fact that the lower half of the pulvinus is relatively the more excitable. Vertical light thus induces a movement in a vertical plane. But an interesting variation of the response occurs under the lateral action of light. A stimulus will be termed *lateral* when it acts on either the right or left flank of a *dorsiventral* organ.

The present series of experiments was carried out with the leaf of Mimosa, and in order to eliminate the effect of weight, and also to obtain a record of pure torsion, the following device was employed: The petiole was held by a hooked support made of a thin rod of glass, the points of support being the concavity of a smooth surface. Friction and the effect of weight are thus practically eliminated; the hooked support prevented up or down movement and yet allowed perfect freedom for torsional response. This latter is magnified by a piece of stout aluminium wire fixed at right angles to the petiole (fig. 144). The end of the aluminium wire is attached to the short arm of a recording lever; there is thus compound magnification of the torsional movement. The Oscillating Recorder gave successive dots at intervals which could be varied from 20 seconds to 2 minutes. Time-relations of the response can thus be obtained from the dotted record.

The experimental device just described makes possible the study of the effect of various stimuli applied on the flank of the pulvinus including the junction of the upper and lower halves of the organ. The observer standing in front of the leaf is supposed to look at the stem. Torsional response will then appear as a movement either with or

against the hands of a clock. This responsive torsion, right handed or left-handed, will presently be shown to depend on the direction of the incident stimulus.

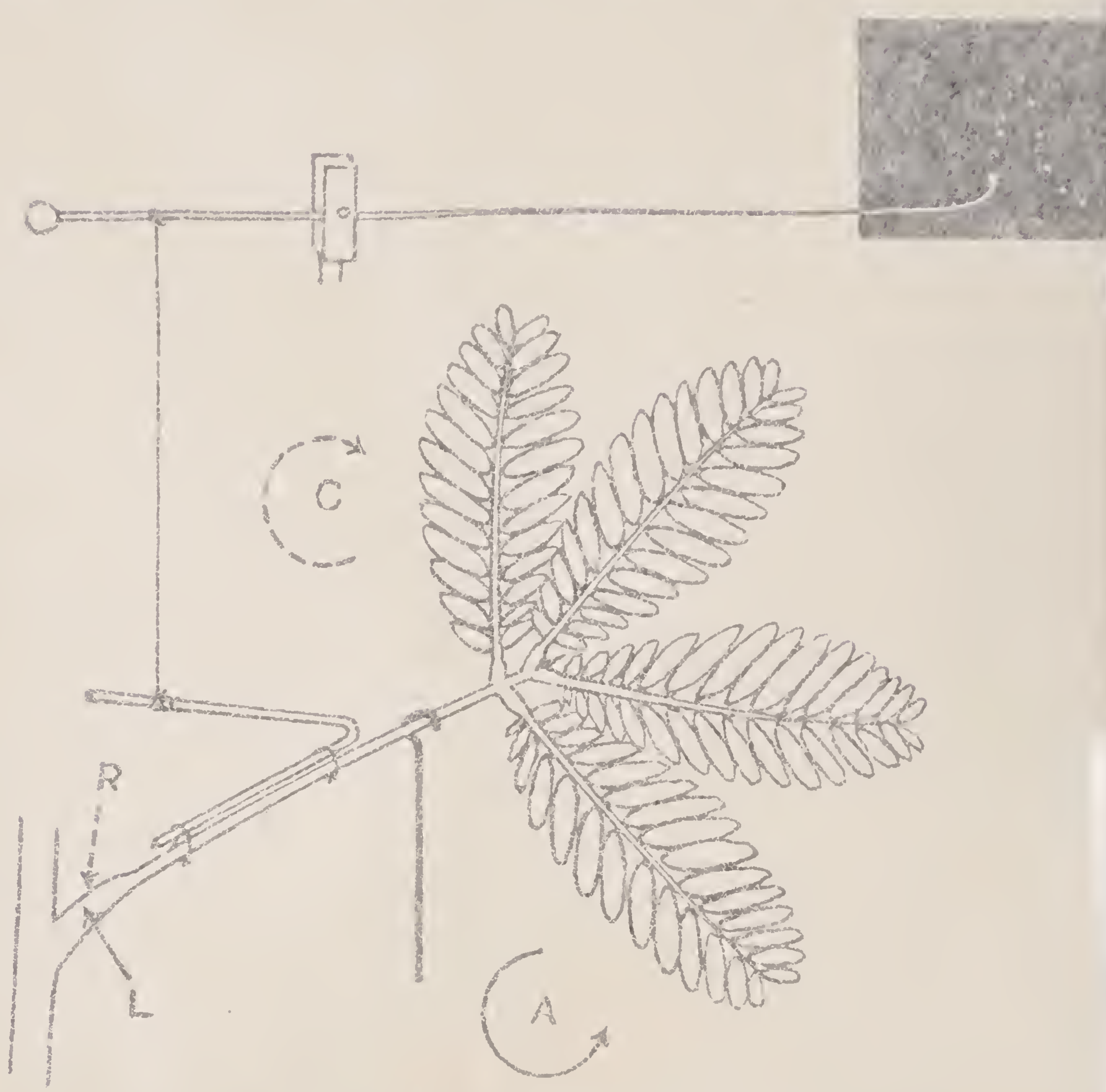


FIG. 14[illegible]. Diagrammatic representation of the Torsional Recorder.

Lateral stimulation, R, applied on right flank (dotted arrow) induces clockwise torsion C (dotted circle). Stimulus, L, applied on left flank (full arrow) induces anti-clockwise torsion A (thick circle).

EFFECT OF LATERAL STIMULATION BY LIGHT

Experiment 135.—The pulvinus of the leaf was stimulated by a horizontal beam of light thrown laterally upon it; the area contiguous to the line of junction of the upper and lower halves of the anisotropic organ responded by differential contraction. When light struck on the

flank, indicated by dotted arrow, the responsive
was clockwise; the responsive reaction thus made *the r and less excitable half of the pulvinus face the stimulus.* 145 gives the record of the torsional response; cessation mulation is followed by recovery.

FIG. 145.

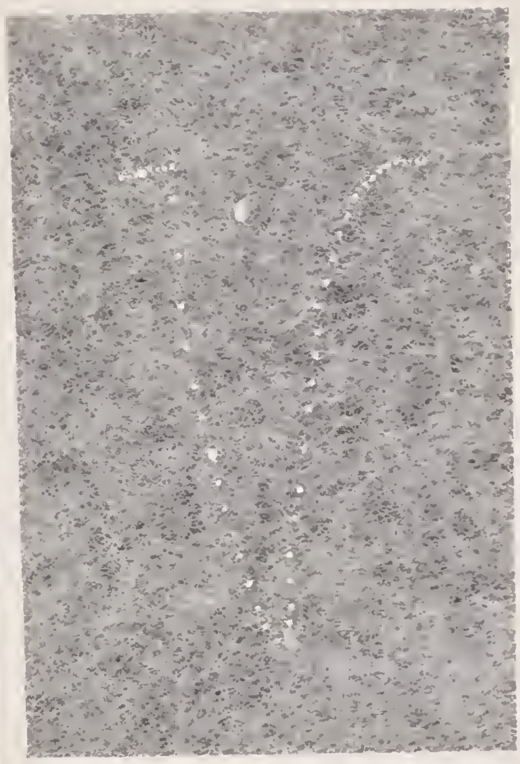


FIG. 146.

FIG. 145. Record of torsional response of pulvinus of Mimosa pudica. Clockwise response to stimulation by light applied on the right flank (up-curve).

FIG. 146. Record of anti-clockwise torsional response to light applied on the left flank (down-curve). Duration of application between two thick dots. Successive dots at intervals of 10 seconds.

DIRECTIVE ACTION OF STIMULUS

Experiment 136.—If now the direction of stimulation e changed so that the light strikes the left flank instead f the right, the torsional response will be anti-clockwise fig. 146). Here also the responsive movement is such that t is the less excitable upper half of the organ that is made to ace the stimulus. It may therefore be concluded that the irection of torsion, clockwise or anti-clockwise, depends on

...tors—namely, the direction of incidence of ...s, and the simultaneous but differential contr... ...t halves of the organ.

Effect of Different Modes of Lateral Stimulation

I proceed to show that torsional response is ind... not merely by the action of light, but by other mod... stimulation as well.

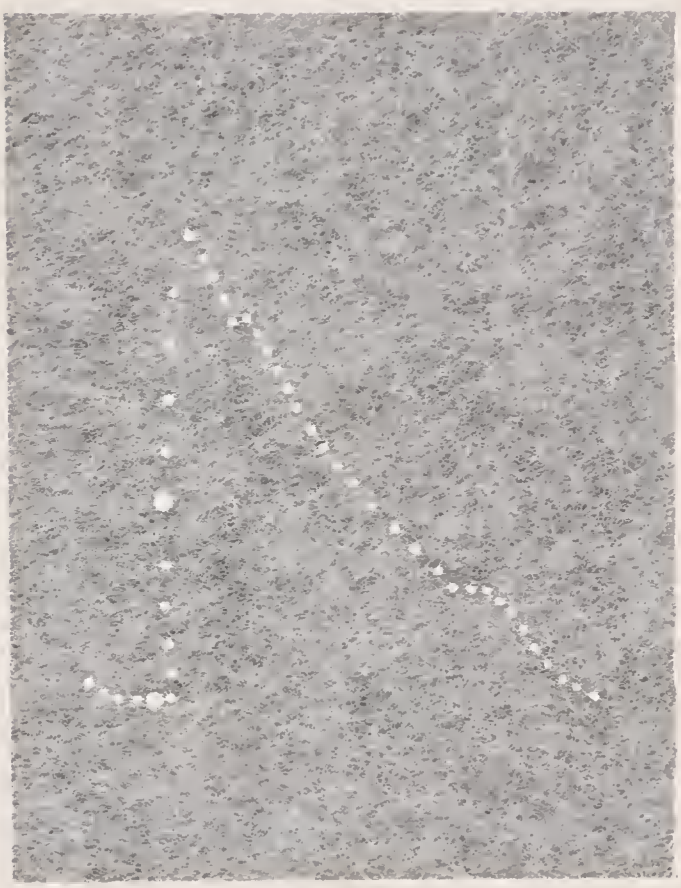


Fig. 147.

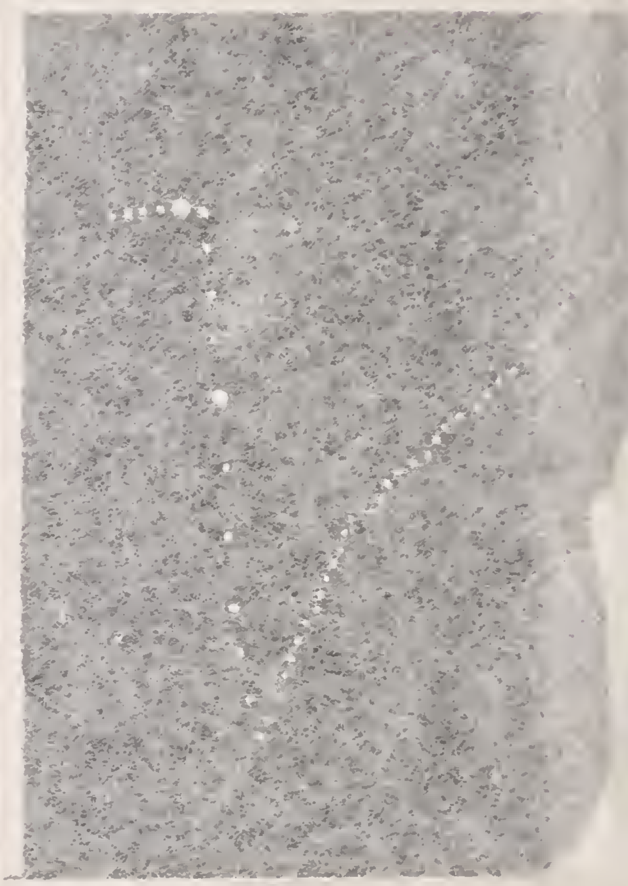


Fig. 148.

Fig. 147. Clockwise torsion under stimulation of right flan... by thermal radiation.

Fig. 148. Anti clockwise torsion under stimulation by therm... radiation applied to left flank. (Mimosa.)

Experiment 137. *Effect of chemical stimulation.*— Dilute hydrochloric acid was at first applied on the le... flank of the pulvinus along the line of junction of the up... and lower halves. This gave rise to a responsive torsion against the hands of the clock. Chemical stimulation of the right flank induced, on the other hand, a torsional moveme...

with the hands of the clock. Here also the direction of stimulus is found to determine the direction of responsive torsion.

Experiment 138. *Effect of lateral stimulation by thermal radiation.*—I next employed thermal radiation as the stimulus: the source of radiation was a length of electrically heated platinum wire. It is advisable to interpose a shield with a narrow horizontal slit, so as to localise the stimulus at the junction of the upper and lower halves of the pulvinus. The effectiveness of radio-thermal stimulus being great, the response was very pronounced. Stimulus applied at the right flank induced right-handed or clockwise torsion (fig. 147); application at the left flank gave rise to left-handed or anti-clockwise torsion (fig. 148).

Geotropic stimulus.—The stimulus of gravity induces similar responsive torsion which is determined by the direction of the incident stimulus. This will be fully described in a subsequent chapter.

Effect of Differential Excitability on the Direction of Torsion

Under normal conditions the torsional response to light places the upper surface of the leaf or leaflet at right angles to the incident light. That this movement is not due to some specific sensibility to light is shown by the fact that all modes of stimulation—chemical, thermal and others—induce similar responsive torsion. The torsional response is determined not only by the direction of the incident stimulus, but also by the differential excitability of the organ. This latter may be reversed by the local application of various depressing agents on the normally more excitable lower half of the pulvinus. Under this treatment the lower half of the pulvinus can be rendered relatively the less excitable. Lateral stimulation by light is now found to induce a torsional movement which is the reverse of the normal, so that the upper surface of the leaf turns away from light.

Teleological advantage cannot, therefore, be the determining factor which causes the directive movement.

In all the instances given above, and under every mode of stimulation, the responsive movement is such as to cause the less excitable half of the pulvinus to face the stimulus.

Laws of Torsional Response

1. An anisotropic organ, when laterally excited by any stimulus, undergoes torsion by which the less excitable side is made to face the stimulus.
2. The intensity of torsional response incre[ases] with the differential excitability; [when] the original difference is reduce[d or] reversed, the torsional response unde[rgoes] concomitant diminution or reversal.

Advantage of the Method of Torsional Resp[onse]

The experimental study of torsional response no[t only] opens a new line of inquiry into the reactions of the [plant] to various stimuli, but it also possesses certain s[pecial] advantages. For instance, in investigations on the resp[onse] of the leaf of Mimosa to light by the ordinary method, th[e] responsive movements in a vertical plane are recorded. The responsive up-movement, induced by light acting from above, is, however, opposed by the weight of the leaf. But in the torsional response, where the leaf is held by a hooked glass support, the movement is free from the complicating factor of the weight of the leaf. The pulvinus of Mimosa, again, occasionally exhibits an autonomous pulsation; in the ordinary method of record the true response to external stimulation may thus be modified by the natural movement of the leaf. But in the torsional method the autonomous up or down movement is restrained by the hooked support and the response to lateral stimulation is unaffected by the spontaneous movement of the leaf. The torsional method,

moreover, opens out possibilities of inquiry in new directions, such as the comparison of the excitatory effects of different stimuli by the Method of Balance.

THE TORSIONAL BALANCE

A beam of light falling on the left flank of the pulvinus of Mimosa initiates a torsion against the hands of the clock. A second beam falling on the right flank initiates a contrary movement; the resultant effect is, therefore, determined by the effective stimulation of the two flanks. The pulvinus thus becomes a delicate indicator by which the effectiveness of two stimuli may be compared with each other. The following experiment is cited as an example of the application of the method of phototropic balance.

Experiment 139.—A parallel beam of light from a small arc-lamp, passing through a blue glass, falls on the left flank of the pulvinus; a beam of blue light also strikes the pulvinus on the right flank, the intensity of the latter being so adjusted that the resultant torsion is zero. The blue glass on the left side is now removed, the unobstructed white light being allowed to fall on the left flank of the pulvinus. This is found to upset the balance, the resultant torsion being anti-clockwise, proving that white light induces greater excitation than blue light. A red glass is now interposed on the left side, with the result that the balance is upset in the opposite direction, showing that the phototropic effect of red light is comparatively feeble. It is thus possible to compare the tropic effect of one form of stimulation with that of another. It is enough here to draw attention to the various investigations rendered possible by the Method of Torsional Balance. Examples of some of these will be given in a subsequent chapter.

SUMMARY

Lateral stimulation induces a torsional response in a dorsiventral organ. This is true of all modes of stimulation.

The responsive torsion is determined by the direction of the incident stimulus, and by the differential excitability of two halves of the organ, the torsion being such that the less excitable half of the organ is made to face the stimulus.

The twist exhibited by various leaves and leaflets under light finds its explanation in the demonstrated laws of torsional response.

The direction of an incident stimulus may be determined from the responsive torsion of a dorsiventral organ.

The Method of Torsional Balance permits of comparison of the excitatory efficiency of two different stimuli which act simultaneously on opposite flanks of the organ.

CHAPTER XXIV

THE AFTER-EFFECT OF LIGHT

Two types of diurnal movement have been considered: one in response to the predominant effect of variation of light, and the other to that of changing temperature. There are, however, certain other organs which are sensitive to variations both of light and of temperature. The effect of light is, generally speaking, antagonistic to that of rise of temperature; hence the movement which is the resultant of the two effects requires careful analysis.

Still greater complexity is introduced by the conflicting factors of the immediate and the after-effect of light. Great obscurity surrounds this after-effect phenomenon, and I endeavoured to determine its characteristics by the electric method of investigation. A fuller account of the after-effect of light on the response of various plant-organs and of the animal retina will be found elsewhere.[1] I here refer only to one or two characteristic results which have immediate bearing on the present subject.

Direct stimulation by light induces an excitatory reaction, which is exhibited mechanically by contraction and electrically by induced galvanometric negativity. Under continuous stimulation the excitatory effect, whether of positive curvature or of induced galvanometric negativity, is found to attain a maximum. The positive tropic curvature and the induced galvanometric negativity exhibit, on account of fatigue at the directly stimulated proximal side, a decline and neutralisation. This neutralisation is

[1] *Comparative Electro-Physiology*, p. 302.

further favoured by transverse conduction of excitation to the distal side (p. 134).

The character of the after-effect will presently be shown to be modified by the duration of the antecedent stimulation, the different phases of which will, for convenience, be distinguished as pre-maximum, maximum, and post-maximum.

Determination of After-Effect by Electric Response

Confining attention for the present to indications given by the electric response, it is found that under continued action of light the excitatory galvanometric negativity increases to a maximum, after which there is a decline and neutralisation. Fig. 149 gives the galvanographic record of the electric response of the leaf-stalk of Bryophyllum to light; the up-curve represents increasing negativity which, after attaining a maximum, undergoes neutralisation as seen in the down-curve. Fig. 150 exhibits the various after-effects on sudden stoppage of light at three different stages—before the attainment of maximum, at the maximum, and after the maximum. Light is applied at arrow.

Experiment 140. *After-effect of pre-maximum stimulation.*—Continuous stimulation induces increasing galvanometric negativity. When stimulus is stopped at *a* before response reaches the maximum, the after-effect is a persistence of excitatory galvanometric negativity, which carries the response record higher up, after which recovery takes place and the record returns to the zero-line of normal equilibrium. The after effect of pre-maximum stimulation is thus a short lived continuance of the response followed by recovery (fig. 150).

Experiment 141. *After-effect at maximum.*—In this case the photic stimulation was continued till the attainment of maximum, when light was suddenly removed at *b*. The

after-effect was no longer a persistence of the negative response, but disappearance of negativity and recovery to zero-line of equilibrium at *c* (fig. 150).

FIG. 149. FIG. 150.

FIG. 149. Electric response of the petiole of Bryophyllum under continuous photic stimulation. Increasing negativity represented by up curve, neutralisation by down-curve.

FIG. 150. Semi-diagrammatic representation of electric after-effects due to photic stimulation.

Pre maximum stimulation, produced by stoppage of light at *a*, gives rise to continuation of previous response followed by recovery.

Stoppage of light at maximum, *b*, gives rise to recovery to equilibrium position *c*.

Stoppage of light at post maximum, *c*, gives rise to overshooting below zero-line, as seen in the dotted record, *cd*

Experiment 142. *After-effect at post-maximum.*—In this case the light was continued till there was complete neutralisation at *c*, the curve of response returning to zero-line; to all outer seeming the responsive indication of the organ is the same as before excitation. But stoppage of stimulation at *c* caused an overshooting at a rapid rate far *below* the zero-line (fig. 150).

The condition at post-maximum *c* is thus one of dynamic equilibrium where two opposite activities 'A' and 'D' balance each other: for had the condition of the 'neutralised' organ been exactly the same as when it was fresh, cessation of stimulus would have kept the galvanometric spot of light at the zero-position.

The electric investigations described above indicate that the after-effect is modified by the duration of stimulation and that:

1. The after-effect of pre-maximum stimulation is the continuation of response in the original direction (upwards, and away from the zero-line), followed by recovery;
2. The after-effect of maximum stimulation is a recovery towards zero-position; and
3. The after-effect of post-maximum stimulation is an overshooting of response *downwards*, below the zero-line.

Tropic Response to Light and its After-Effect

I next describe the after-effects of light exhibited by mechanical response, the results of which will be found to be parallel to those given by electric response. The specimen employed was the terminal leaflet of *Desmodium gyrans*, the pulvinus of which is very sensitive to light. Pulvinated organs, generally speaking, exhibit a diurnal variation of turgor, in consequence of which the position of the equilibrium of the leaf or leaflet undergoes a periodic change. The equilibrium position, however, remains fairly

constant for nearly 2 hours about midday, the variation of temperature at this period being slight. The pure effect of light can be obtained by carrying out the experiment during this period, and thus complications which may arise from autonomous pulsation are also avoided.

The duration of the experiment may be shortened by the choice of a suitable intensity of light; a given tropic effect induced by prolonged feeble light may thus be obtained by short exposure to stronger light. The source of light in the following experiment was a 50-candle-power incandescent lamp. The intensity was increased to a suitable value by focusing the light on the upper half of the pulvinus by means of a lens. The intensity was so adjusted that the maximum positive curvature occurred in the course of about 6 minutes, and complete neutralisation was attained after an exposure of 17 minutes.

Experiment 143. *After-effect at pre-maximum.*—Light was allowed to act on the upper half of the pulvinus for 2 minutes and 20 seconds; this induced an up-movement, *i.e.* a positive curvature. On the stoppage of light the up-movement continued for 1 minute and 20 seconds, after which the down-movement of recovery was completed in 6 minutes and 20 seconds (fig. 151). The immediate after-effect is thus a movement upward, away from the zero-line of equilibrium. The result is seen to agree with the electric after-effect of pre-maximum stimulation.

Experiment 144. *After-effect at maximum.*—Application of light for 5 minutes and 20 seconds induced a maximum positive curvature. Stoppage of light was followed at once by recovery, which was completed in about 10 minutes (fig. 152).

Experiment 145. *After-effect at post-maximum.*—As the plant was fatigued by previous experiments, a fresh specimen was taken and light was applied continuously on the upper half of the pulvinus. This gave rise first to a maximum positive curvature; neutralisation took place after application of light for 17 minutes. On the stoppage

of light there was a sudden overshooting *below* the zero-line (fig. 153); the rate of the movement on the cessation of light was nearly twice as quick as during the process of neutralisation.

I also obtained a very interesting record of the post-maximum after-effect of light with *Cassia alata*.

FIG. 151. FIG. 152. FIG. 153.

FIG. 151. Light applied at arrow, and stopped at the second arrow within a circle. After-effect of pre-maximum stimulation is continuation of positive curvature followed by recovery.

FIG 152. After-effect of stimulation at maximum; recovery towards zero-position of equilibrium.

FIG. 153. After-effect of post-maximum stimulation is a rapid overshooting below the position of equilibrium.

Light was applied in all cases on upper half of pulvinus of terminal leaflet of Desmodium gyrans.

Experiment 146.—In Cassia, as in Mimosa, light acting from above induces at first an erectile movement of the leaf which reaches a maximum, after which there follow neutralisation and reversal. In the record given (fig. 154), light from a small arc-lamp acting on the upper half of the pulvinus for 48 minutes induced the maximum positive curvature; this was completely neutralised by further exposure to light for 20 minutes; cessation of light was followed by a rapid fall of the leaf beyond the position of

equilibrium, the responsive after-effect being more rapid than under light. The after-effect of prolonged exposure

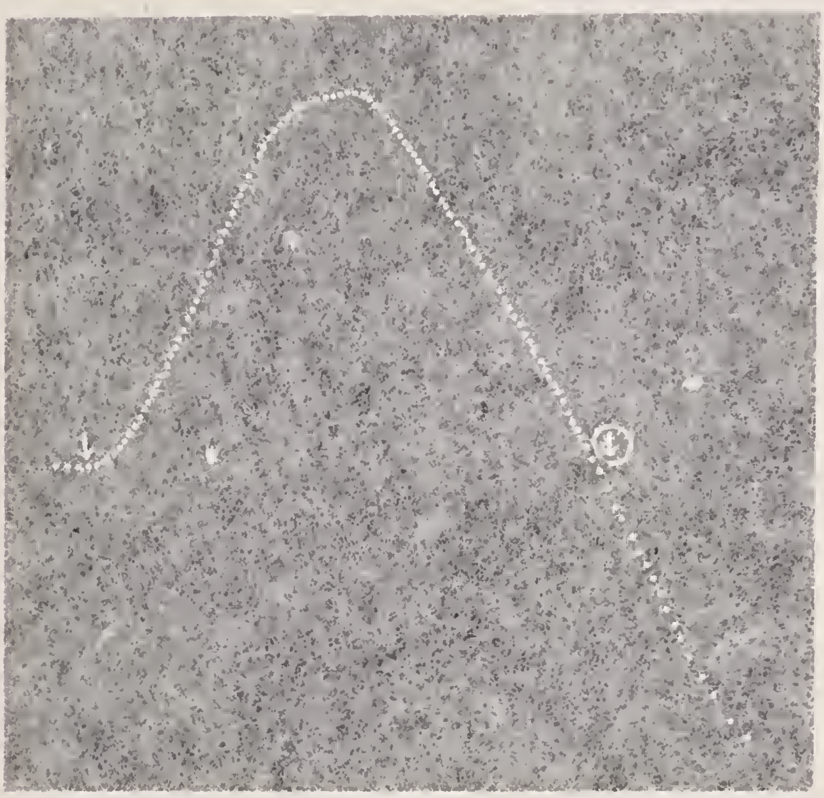


FIG. 154. Post maximum after-effect of light on response of leaf of Cassia.

There is an overshooting on cessation of light at arrow within a circle.

is thus an 'overshooting' beyond the normal position of equilibrium.

SUMMARY

The after-effect of light is modified by the duration of the exposure.

Under continued action of light, the electric response of galvanometric negativity in plants attains a maximum, after which it undergoes decline and neutralisation.

The electric after-effect exhibits characteristic differences depending on the duration of the previous exposure to light.

The pre-maximum after-effect is a temporary continuation of the response induced by light followed by recovery.

The after-effect at maximum is an immediate recovery to the normal equilibrium.

The after-effect at post-maximum is an overshooting below the position of equilibrium.

The mechanical effects and after-effects of light are similar to the corresponding electric effects. The pre-maximum after-effect is a continuation of positive tropic movement followed by recovery; the after-effect at maximum is a recovery to the normal position of equilibrium; the post-maximum after-effect is an overshooting, that is, a fall to below the normal position.

CHAPTER XXV

THE DIURNAL MOVEMENT OF THE LEAF OF MIMOSA

The thermo-geotropic record of diurnal movement of plants described in a previous chapter consists of an up-curve from thermal noon to thermal dawn, and of a down-curve from thermal dawn to thermal noon. The responding organ, whether an inclined stem or a horizontally placed petiole, underwent an erection during the decline of temperature, and a fall with the rise of temperature. The diurnal record of the Mimosa leaf appears, however, to be totally different; this apparent difference arises from the presence of fresh complicating factors, inasmuch as the leaf is sensitive not only to variation of temperature but also to changes of light.

Experiment 147. *Diurnal record of Mimosa.*—I took the diurnal record of Mimosa (fig. 155) for 24 hours, commencing at 2 P.M., which is the thermal noon. The summer and winter records are essentially the same, the only difference being the greater vigour of movement exhibited by summer specimens. The diurnal movement of the leaf is very definite and characteristic, for the curves obtained for several years in succession are found to be quite concordant. The record may conveniently be divided into four phases.

First phase.—The leaf erects itself after thermal noon until 5 or 5.30 P.M. The temperature, it should be remembered, is undergoing a fall during this period.

Second phase.—There is a sudden fall of the leaf in the evening, which continues till 9 P.M. or thereabout.

Third phase.—The leaf erects itself till thermal dawn at about 6 A.M. next morning.

Fourth phase.—There is a fall of the leaf during the rise of temperature from thermal dawn to thermal noon.

FIG. 155. Diurnal record of leaf of Mimosa in summer and in winter. Leaf rises from 2 to 5 P.M., when there is a spasmodic fall. Leaf re-erects itself from 9 P.M. to 6 A.M., after which there is a gradual fall till 2 P.M. with pulsation. The uppermost record gives temperature variation, up-curve representing fall of temperature and *vice versa*.

The uniformity of the fall is, however, interrupted by one or more pulsations in the forenoon, which are more frequent in summer than in winter.

It will thus be seen that the difference between the

typical thermo-geotropic curve and the curve of Mimosa is not so great as appears at first sight, with the exception of the spasmodic fall in the evening. I will presently explain the reason of the sudden fall in the evening, and of the multiple pulsations in the forenoon.

It is possible to trace a continuity between the typical thermo-geotropic reaction and the characteristic diurnal movement of the leaf of Mimosa which is affected by light. The young leaves which expand at the beginning of spring take some time to become adjusted to the diurnal variation. There are two intermediate stages through which the leaves pass before they exhibit their characteristic diurnal curve. Slow rhythmic pulsations are at first seen to occur during day and night. At the next stage the leaves exhibit the diurnal movement of fall from thermal dawn to thermal noon, and that of erection from thermal noon to thermal dawn next morning, the record being in every way similar to the typical thermo-geotropic curve. It is only at the final stage of development of the leaf that there is the spasmodic fall in the evening, which will be shown to be a characteristic post-maximum after-effect of light.

The complexity of the diurnal movement of Mimosa arises from the fact that there are three factors whose fluctuating effects are different at various hours of the day. The position at any particular hour results from the algebraical summation of the effects of the following factors: (1) the thermo-geotropic reaction; (2) the autonomous pulsation of the leaf; (3) the immediate effect of light; and (4) its after-effect. I will take up the detailed consideration of the subject in the following order:

1. *The thermo-geotropic reaction.*—A crucial experiment is described later which demonstrates the thermo-geotropic effect in the diurnal movement of the leaf.

2. *Autonomous pulsation of Mimosa.*—The natural pulsation of the leaf is obscured by the paratonic effect of external stimulation. The occurrence of pulsatory response in the morning record (*see* fig. 155) led me to search for

multiple activity of the pulvinus. I found that the very young leaves in spring exhibited automatic pulsation throughout day and night; in older leaves, tuned to diurnal periodic movements, these natural pulsations are more or less suppressed, but several pulsations may be exhibited in the forenoon even by mature leaves (fig. 156).

3. *The immediate effect of light.*—This is not constant, but will be shown to undergo a definite variation with the

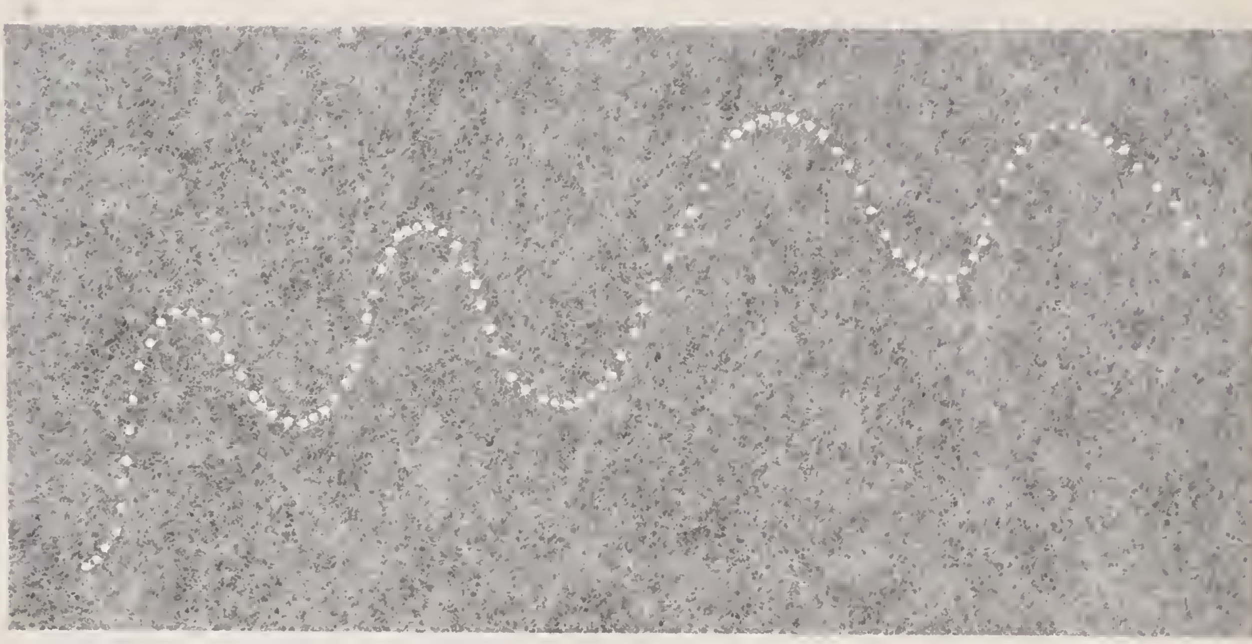


FIG. 156. Record of automatic pulsation of Mimosa leaf in the forenoon. Average period 25 minutes.

Successive dots at intervals of a minute.

intensity and duration of light. The great difficulty of recording the change of intensity of light was overcome by the construction of the Radiograph already described (p. 197). I reproduce a record (fig. 157) obtained in my greenhouse on March 5, 1919, which gives a general idea of the variation of light from morning to evening; the record shows that light began to be perceptible at 5.30 A.M., and that the intensity increased rapidly and continuously till it reached a climax at noon, after which it began to decline slowly. The fall of intensity was very abrupt after 5 P.M., the effect being reduced to zero at 6.30 P.M.

4. *The after-effect of light.*—The after-effect is greatly modified by the intensity and duration of the illumination,

which give rise to the characteristic responses—the pre-maximum, the maximum, and the post-maximum.

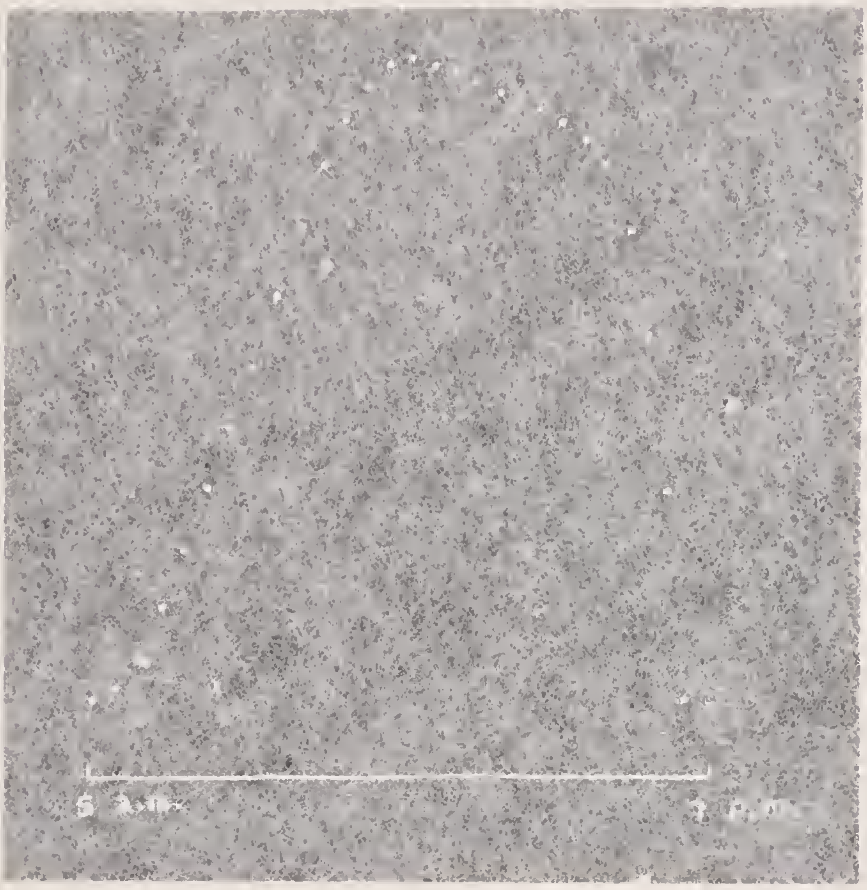


FIG. 157. Photometric record showing the variation of intensity of light from morning to evening.
Successive dots are at intervals of 30 minutes.

THE SPASMODIC FALL OF THE LEAF

Pfeffer regarded the fall of the leaf which occurs abruptly late in the afternoon as due to the increased mechanical moment of the secondary petioles moving forward on withdrawal of light. I proceed to show that this characteristic movement occurs even after complete removal of the sub-petioles, so that an increased mechanical moment cannot be the true explanation of the fall.

Experiment 148. *Diurnal movement of the petiole after removal of sub-petioles.*—In this experiment the possibility of any variation of mechanical moment was obviated by cutting off the end of the petiole, which carried the sub-petioles. The cut end was coated with collodion flexile to prevent evaporation. The intense stimulation caused by the amputation induced excitatory fall of the leaf, but

it recovered its normal activity after a period of 3 hours or so. The diurnal record of the leaf was commenced shortly after 1 P.M., it will be noticed that the leaf, though deprived of the weight of its sub-petioles, still exhibited a sudden fall at about 5 P.M. (fig. 158). The fall of the leaf cannot therefore be due to increased mechanical moment. The effect of weight was moreover, eliminated in another experiment on torsional response (Experiment 149), which also exhibited a sudden movement of the leaf after 5 P.M.

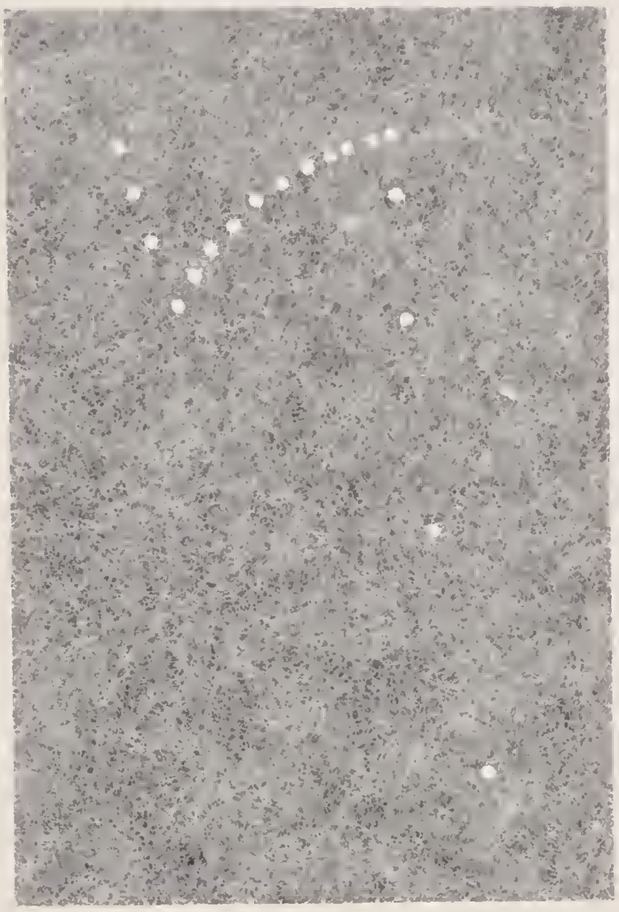


FIG. 158. Record of leaf of Mimosa after removal of sub-petioles. The leaf fell up to 2.30 P.M., and then rose till 5 P.M., after which there was a spasmodic fall.

Successive dots at intervals of 15 minutes.

Pfeffer, in his 'Entstehung der Schlafbewegung' (1907), has offered another explanation of the sudden fall of the leaf of Mimosa. This, according to him, is not the direct effect of diminished intensity of light in the evening, but is due to the release of the leaf from the phototropic action of light, which, so long as it is sufficiently intense, holds the leaf in the normal position with its upper surface at right angles to the incident rays. On being set free from the strong action of light, the leaf moves in accordance with the preceding condition of tension; and as this is low, the leaf falls, soon to rise again as the tension increases in prolonged darkness.

The above explanation presupposes (1) that the tension continuously decreases till the evening; and (2) that as soon as the phototropic restraint which holds the leaf up is removed, it falls down in accordance with the prevailing diminished tension.

Referring to the first point, an inspection of the diurnal curve of Mimosa shows that the leaf had no natural tendency to fall towards the evening. There was, on the contrary, a movement of erection, on account of fall of temperature after the thermal noon (*cf.* fig. 155). As the natural tendency of the leaf was to erect itself, removal of phototropic restraint cannot be the cause of the movement of fall.

The following experiment not only exhibits the diurnal curve of an intact plant, but also clearly demonstrates the thermo-geotropic effect, as well as the immediate and the after-effect of light.

Diurnal Variation of Geotropic Torsion

I have already demonstrated the torsional response under unilateral stimulation by light. I shall also show in a later chapter that similar torsional response is obtained under the stimulus of gravity (p. 307).

When a Mimosa plant is laid down sideways, so that the plane of junction between the upper and the lower halves of the pulvinus is vertical, geotropic stimulus acts laterally on the two differentially excitable halves of the pulvinus. When the less excitable upper half is to the left of the observer, the responsive torsion under geotropic stimulus is clockwise, the less excitable upper half of the pulvinus being thereby made to face the vertical lines of gravity. When the plant is turned over to the other side (the less excitable upper half being now to the right of the observer), the induced torsion is counter-clockwise. It has been shown that lateral stimulation by light gives rise to torsion; when light acts in the same direction as the stimulus of gravity, *i.e.* from above, there is an enhancement of the rate of torsion, the resulting curve of response being due to the joint effects of light and gravity.

Experiment 149.—I obtained a 24 hours' record of the variation of torsional response in the leaf of Mimosa, commencing with thermal noon at 2 P.M. It is to be borne in

mind that increase of torsion corresponds with the erectile movement of the leaf in the diurnal thermo-geotropic curve. Inspection of fig. 159 shows that the fall of temperature after thermal noon at 2 P.M. was attended by an increase of torsion. The curve went up till about 5 P.M., as in the ordinary record of Mimosa. The torsion suddenly decreased under rapid diminution of light after 5 P.M. The torsion

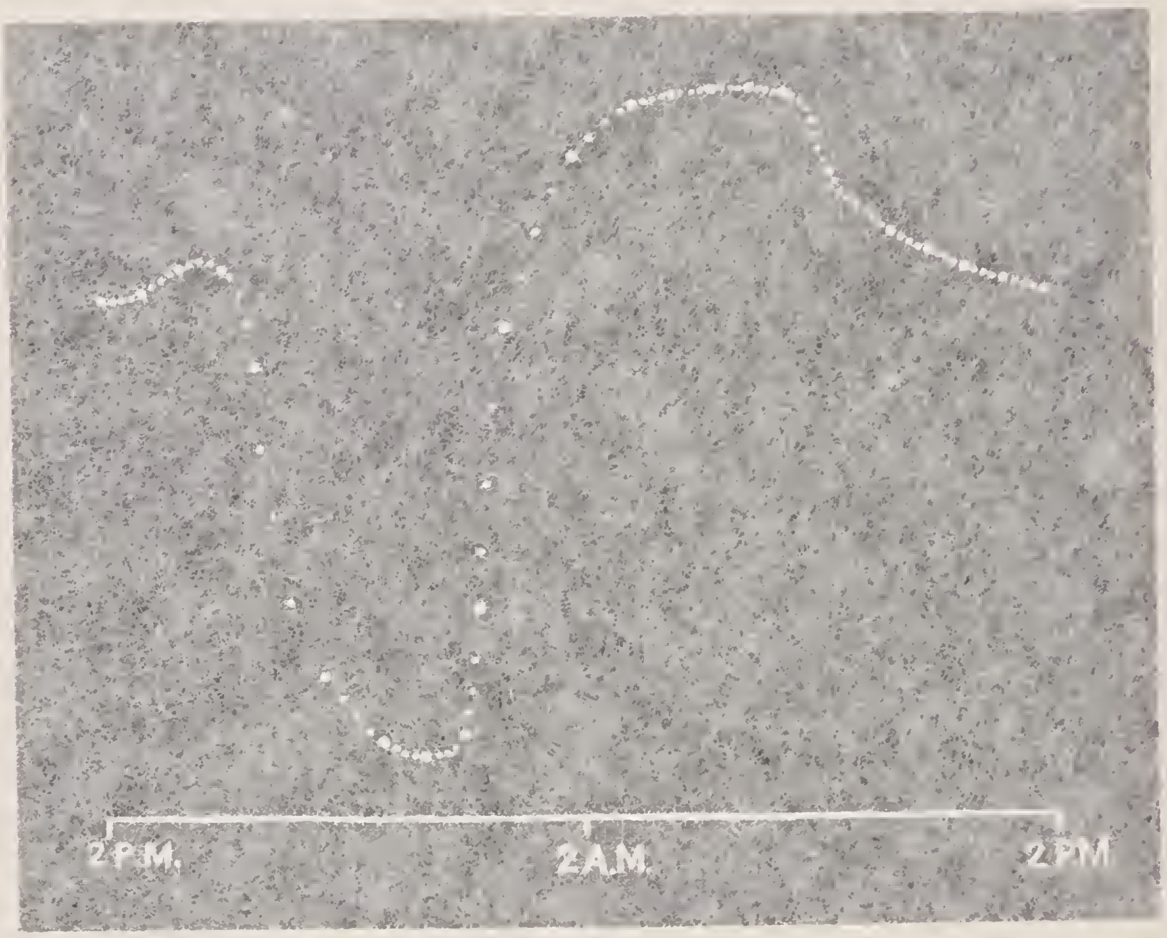


FIG. 159. Record of diurnal variation of geotropic torsion in Mimosa leaf.

Up-curve represents increase, and down-curve decrease of torsion.

then increased with falling temperature from 6 P.M. till thermal dawn next morning. After 6 A.M. there was a continuous diminution of torsion till 2 P.M.

The diurnal variation of geotropic torsion exhibited by Mimosa may be summarised as follows: The torsion undergoes periodic increase during the fall of temperature from afternoon till next morning, and diminution during rising temperature from morning till afternoon. A sudden diminution of torsion occurs at about 5 P.M., due to the disappearance of light. The torsional record is, to all intents and purposes,

a replica of the record of the periodic up and down movements of the leaf.

This method of torsional response has a very important advantage over that of the ordinary method, since, the petiole being supported by a loop of wire, the weight of the leaf can have no effect on the curve of response.

The Characteristic After-Effects of Light

In the previous chapter it was shown (p. 265):

1. That the pre-maximum after-effect is a temporary continuation of the response induced by light followed by recovery;
2. That the after-effect at maximum is an immediate recovery to the normal equilibrium; and
3. That the after-effect at post-maximum is an over-shooting below the position of equilibrium.

Consideration of these results will be found to explain the various anomalies in the diurnal movement of the leaf of Mimosa.

Effect of Artificial Darkness

Experiment 150.—Successive records were taken of the effect of artificial darkness for 2 hours, alternating with exposure to light for the same time. The plant was subjected to darkness by placing a piece of black cloth over the glass case in which it was enclosed, from 12 to 2 P.M.; it was exposed to light from 2 to 4 P.M., and then subjected to darkness once more from 4 to 6 P.M.

The record given in fig. 160 shows that the leaf had been moving upwards under the action of light (positive phototropism); the moment of exposure to darkness is marked with a thick dot in the record. *The after effect of the withdrawal of light is seen to be a movement in the same direction as that under exposure to light*; this persisted for 10 minutes, followed by recovery which was completed by

2 P.M., as shown in the horizontal character of the curve. On restoration of light (at the point marked with the second thick dot) the leaf moved upwards till the positive phototropic movement attained a maximum in the course of 1 hour and 30 minutes, after which neutralisation set in, and

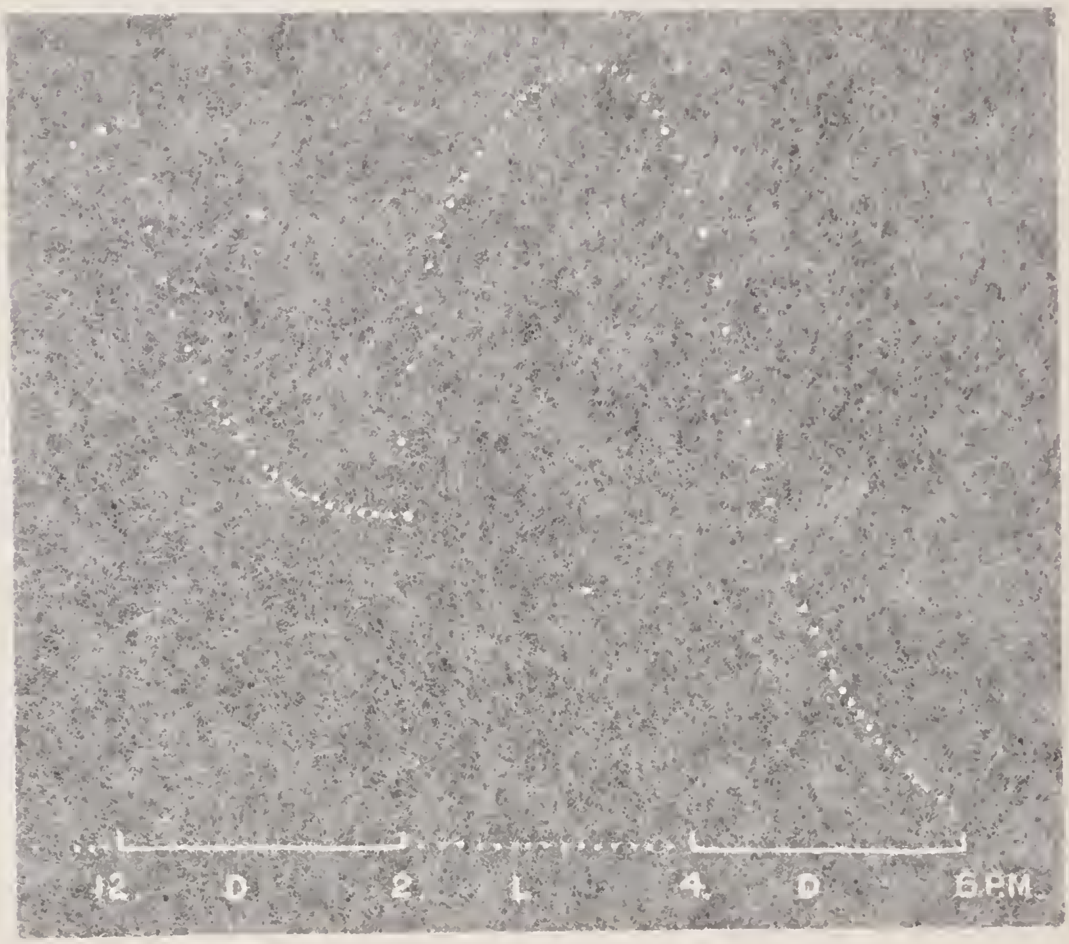


FIG. 166. Effect of periodic alternation of darkness D, light L, and of darkness D, on the response of Mimosa leaf. The first darkness causes the pre-maximum after effect of slight erection followed by recovery. The subsequent exposure to light from 2 to 4 P.M. caused erectile movement followed by partial neutralisation by 4 P.M. Stoppage of light at the third thick dot caused a sudden fall of leaf below the position of equilibrium.

by 4 P.M. the positive phototropic effect had become partially neutralised. Artificial darkness at the third thick dot caused a rapid down-movement which overshot the position of equilibrium. The difference of after-effect in the forenoon and in the afternoon lies in the fact that in the first case it was a pre-maximum after-effect, whilst in the second case it was a post-maximum after-effect.

The record of the responses of Mimosa just described was obtained in the course of experiments which lasted

for more than 6 hours. In order to remove all misgivings in regard to possible modification of the result by variation of temperature I carried out the following experiments, which were completed in a relatively short time. I have already explained how the duration of experiment can be shortened by suitable increase of the intensity of light. The

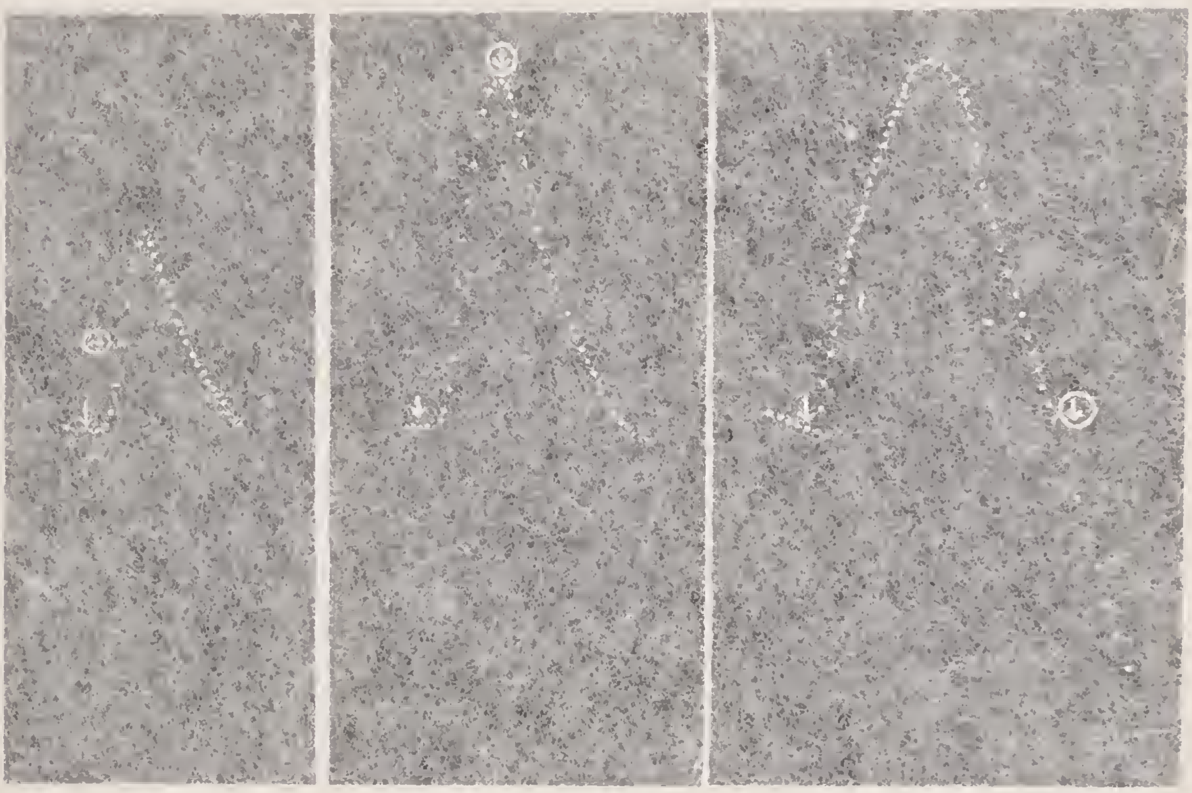


FIG. 161. FIG. 162. FIG. 163.

FIG. 161. Pre-maximum after-effect of light on Mimosa

FIG. 162. After-effect at maximum.

FIG. 163 Post-maximum after effect exhibiting an overshooting below position of equilibrium.

In the above record light was applied at arrow, and stopped at the second arrow enclosed in a circle.

following experiments were commenced inside a room at noon and completed by 2 P.M., so that the temperature variation during this period did not exceed 1° C.

Experiment 151. *After-effect at pre-maximum.*—Light from a 100-candle-power incandescent lamp was focused on the upper half of the pulvinus of Mimosa for 8 minutes, after which the light was turned off. The after-effect was a persistence of previous movement followed by recovery to normal (fig. 161).

Experiment 152. *After-effect at maximum.*—Continued exposure to light for 18 minutes induced maximum positive curvature, as seen in the upper part of the curve becoming horizontal. On the withdrawal of light, there was recovery to the original position of equilibrium (fig. 162).

Experiment 153. *After-effect at post-maximum.*—A fresh specimen of the plant was taken for this experiment; it exhibited maximum positive curvature after an exposure of 20 minutes; continued exposure for a further period of 17 minutes produced complete neutralisation, as indicated by return to normal position. Withdrawal of light at this point gave rise to a rapid down-movement (fig. 163) below the equilibrium position.

It is now possible to give a full explanation of the different phases of diurnal movement of the leaf of Mimosa. The fall of the leaf from its highest position commences at thermal dawn at 6 A.M. in the morning and continues till thermal noon at 2 P.M.; this is the thermo-geotropic reaction due to rise of temperature. In the forenoon the phototropic reaction is positive, and the fall of the leaf, due to rise of temperature, is effected in opposition to the response to light. As the temperature begins to fall after 2 P.M., the leaf begins to erect itself, and in the absence of any disturbing factor would continue its up-movement till next morning. But light undergoes rapid diminution after 5 P.M., the after-effect of which is manifested as an 'overshooting' of the leaf in a downward direction. This fall continues till about 9 P.M., after which the leaf erects itself under the thermo-geotropic action of falling temperature, the maximum erection being attained at the thermal dawn at about 6 A.M. next morning.

The peculiarity of the diurnal curve of Mimosa has been shown to be due to the sensitiveness of the leaf to both light and variation of temperature. This conclusion is verified by experiments with other plants similarly sensitive to both photic and thermal variation. Nothing could be more

conclusive in this respect than the remarkable similarity of the diurnal record of Cassia to that of Mimosa.

Diurnal Curve of the Petiole of Cassia alata

Experiment 154.—The leaf of Cassia exhibits, as does the leaf of Mimosa, a slight erectile movement after thermal noon at 2 P.M.; there is then an abrupt fall, due to rapid diminution of light after 5 P.M.; the movement of fall

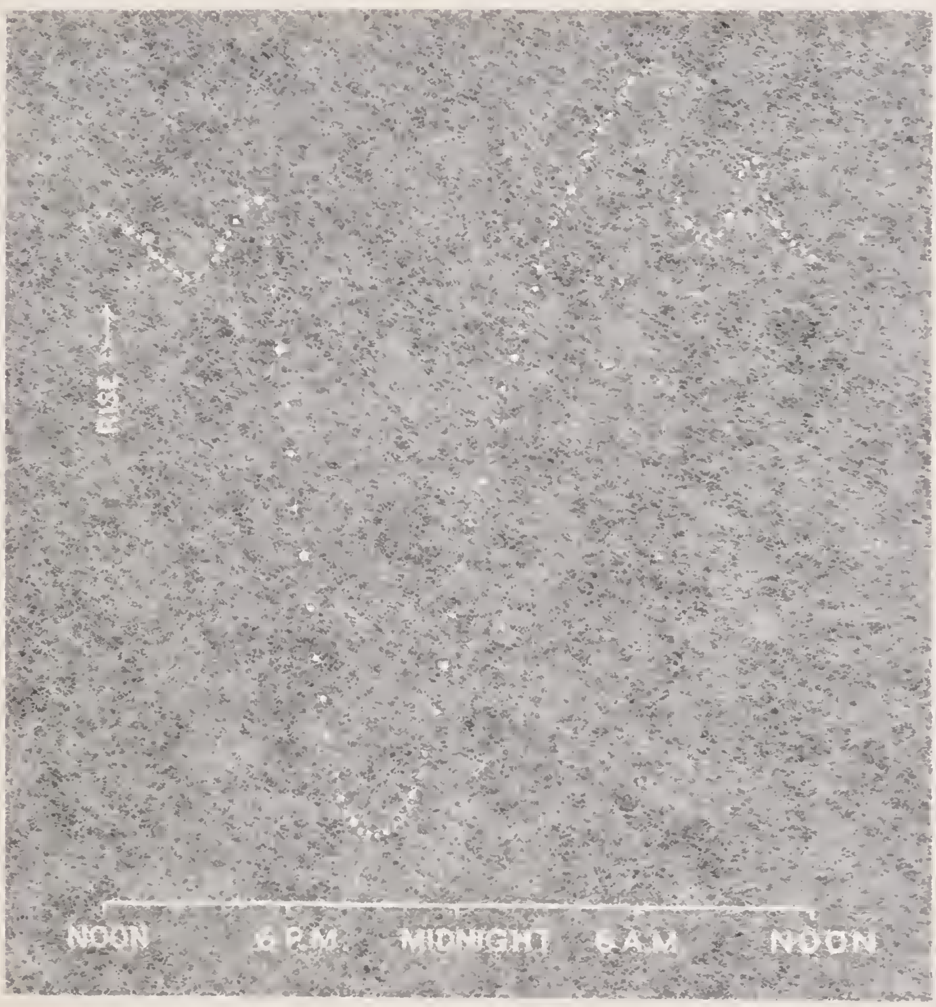


Fig. 164. Diurnal record of Cassia leaf. Note similarity to diurnal record of Mimosa.

continues till about 9 P.M. The leaf then exhibits a continuous rise with the fall of temperature, till the climax is reached about 6 A.M. in the morning; the leaf exhibits later a movement of fall with rise of temperature, there being a number of pulsatory movements in the forenoon evidently due to unstable balance under the opposing reactions to light and to rise of temperature (fig. 164).

Summary

The very complex type of diurnal movement of the primary petiole of Mimosa results from the combined effects of thermo-geotropism and phototropism.

With the exception of a small part of the curve in the evening, the diurnal curve of the leaf is essentially similar to the typical thermo-geotropic curve, exhibiting an erectile movement from thermal noon to thermal dawn, and a fall from thermal dawn to thermal noon.

The torsional response of the leaf of Mimosa exhibits a diurnal variation similar to that exhibited when the leaf is in the normal position.

The leaf of *Cassia alata* exhibits a diurnal movement of the same type as that of Mimosa.

The spasmodic fall of the leaf of Mimosa towards evening is not due to the increased mechanical moment caused by the forward position of the sub-petioles. The record of the leaf with amputated sub-petioles exhibits the same sudden fall in the evening as does that of the intact leaf.

The evening fall of the leaf is shown to be a post-maximum after-effect of light, which causes an over-shooting, the fall of the leaf carrying it below the position of equilibrium.

CHAPTER XXVI

GEOTROPISM

No phenomenon of tropic movement appears so inexplicable as that of geotropism. There are two diametrically opposite responsive movements induced by the stimulus of gravity: in the root a curvature downwards, and in the shoot a curvature upwards. The seeming impossibility of explaining effects so divergent by a single fundamental reaction to stimulation has led to the assumption that the irritabilities of stem and root are of opposite character. I shall, however, endeavour to show that this assumption is quite gratuitous and unnecessary.

Beginning with the simple case of a horizontally laid shoot, the geotropic up-curvature can be explained by one or other of the two suppositions: either (1) that the stimulus of gravity induces contraction of the upper side, or (2) that it induces expansion of the lower side. The second of these two assumptions has found more general acceptance.

In the parallel phenomenon of phototropic curvature, light incident on one side of the shoot induces local contraction and concavity of the directly stimulated proximal side of the organ. Since light is visible there can be no difficulty in ascertaining the exact direction of the incident stimulus and the induced curvature by which the organ tends to place itself parallel to the rays with its apex towards the source of stimulation. But in geotropism the stimulus is invisible, and there is no definite knowledge available about its effective direction in induction of the responsive curvature.

In order to clear away obscurities connected with geotropism it will be necessary to elucidate the following points.

1. The determination of the effective direction of stimulus of gravity. This will be demonstrated by two independent means of inquiry: (1) by the method of algebraical summation of the reaction to geotropic with that to photic stimulation, and (2) by the method of geotropic torsion.

2. The sign of excitation is, as previously explained, a contraction and concomitant galvanometric negativity. Does the stimulus of gravity, like stimulus in general, induce this characteristic excitatory reaction?

3. What is the law relating to the 'directive angle' and the resulting geotropic curvature? By the directive angle (sometimes referred to as the angle of inclination) is meant, as previously explained, the angle which the direction of the stimulus makes with the responding surface.

4. Finally, it is necessary to investigate whether the assumption of opposite irritabilities of the root and the shoot is really justified. If not, the opposite curvatures exhibited by the two organs have to be explained.

I propose in this and in the following chapters to describe the investigations sketched above, employing two independent methods of inquiry—namely, those of mechanical and of electric response. I describe first the automatic method that has been devised for an accurate and magnified record of geotropic movement and its time-relations.

The Geotropic Recorder

The Recorder shown (fig. 165) is very convenient for the study of geotropic movement. The apparatus is four-sided, and it is thus possible to obtain four simultaneous records with different specimens under identical conditions. The recording levers are free from friction with the recording surface. By an appropriate clockwork mechanism the levers are pressed for a fraction of a second against the

recording surfaces. The successive dots in the records may, according to different requirements, be at intervals varying from 5 to 20 seconds. The records therefore not

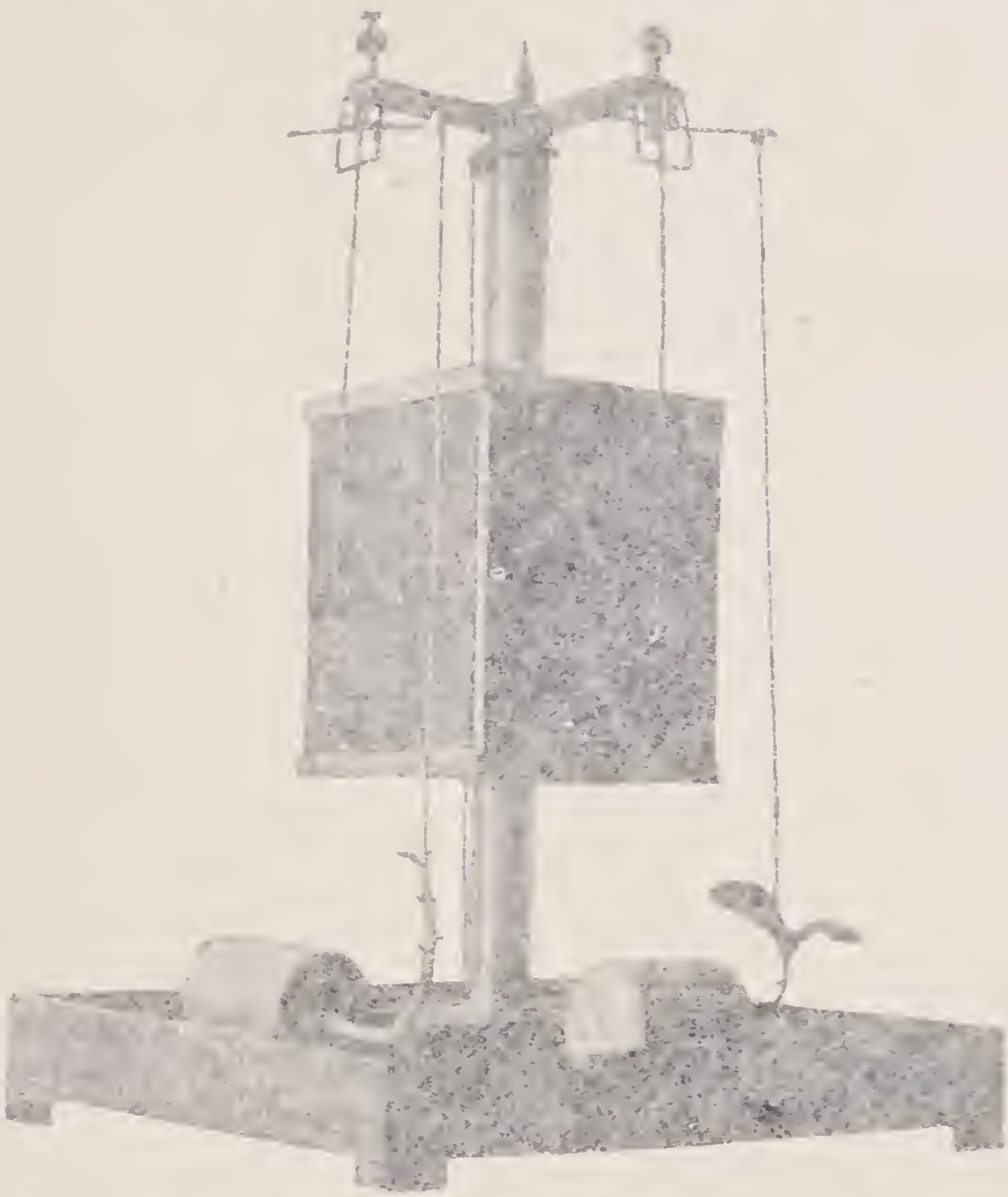


FIG. 165. The Quadruplex Geotropic Recorder

only give the characteristic curves of the geotropic movements of different plants, but also their time-relations. For certain experiments I employ the high magnification of 100 times; a smaller magnification is, however, sufficient for general purposes.

DETERMINATION OF THE CHARACTER OF GEOTROPIC REACTION

The observed geotropic convexity of the upper side of a horizontally laid shoot may be due to excitatory *contraction* of that side, or it may result from compression due

to the active responsive *expansion* of the lower side. The crucial test of excitatory reaction under geotropic stimulation is furnished by the geo-electric response. When a shoot is displaced from the vertical to the horizontal position, *the upper side of the organ is found to undergo an excitatory electric change of galvanometric negativity* indicative of diminution of turgor and *contraction* (p. 315). The tropic effect of geotropic stimulation is thus similar to that of any other mode of stimulation, *i.e.* a contraction of the directly stimulated side, which in the present case is the upper side. The vertical lines of force of gravity impinge on the upper side, and the effective direction of geotropic stimulus is therefore the same as the vertical lines of force indicated by the movement of falling bodies from above to the centre of the earth. The effective direction of geotropic stimulus inferred from the above considerations is fully confirmed by experimental results (p. 308).

It has been explained that excitatory electric response is manifested even in the absence of mechanical expression of excitation; and under geotropic stimulation a firmly held shoot gave the response of a galvanometric negativity of the upper side (p. 317). Hence the fundamental reaction to geotropic stimulation is excitatory *contraction*, as under other modes of stimulation.

Determination of the Latent Period

As regards the interpretation of the record of geotropic movement, it should be borne in mind that after the perception of stimulus a certain time must elapse before the induced growth-variation will result in curvature. There is again another factor which causes delay in the exhibition of true geotropic up-movement: the up-movement of a shoot, in response to the stimulus of gravity, has to overcome the opposition offered by its weight. On account of the bending due to weight there is a greater tension on the upper side, which, as already mentioned (p. 60), enhances

the rate of growth, and thus tends to make that side convex. There is thus an undue delay in the exhibition of geotropic response by induced contraction of the excited upper side. In these circumstances I tried to discover specimens in which the geotropic action would be quick, and in which the retarding effect of weight could be considerably reduced.

Experiment 155. *Geotropic response of the peduncle of Tuberose.*—For this I took a short length of peduncle of

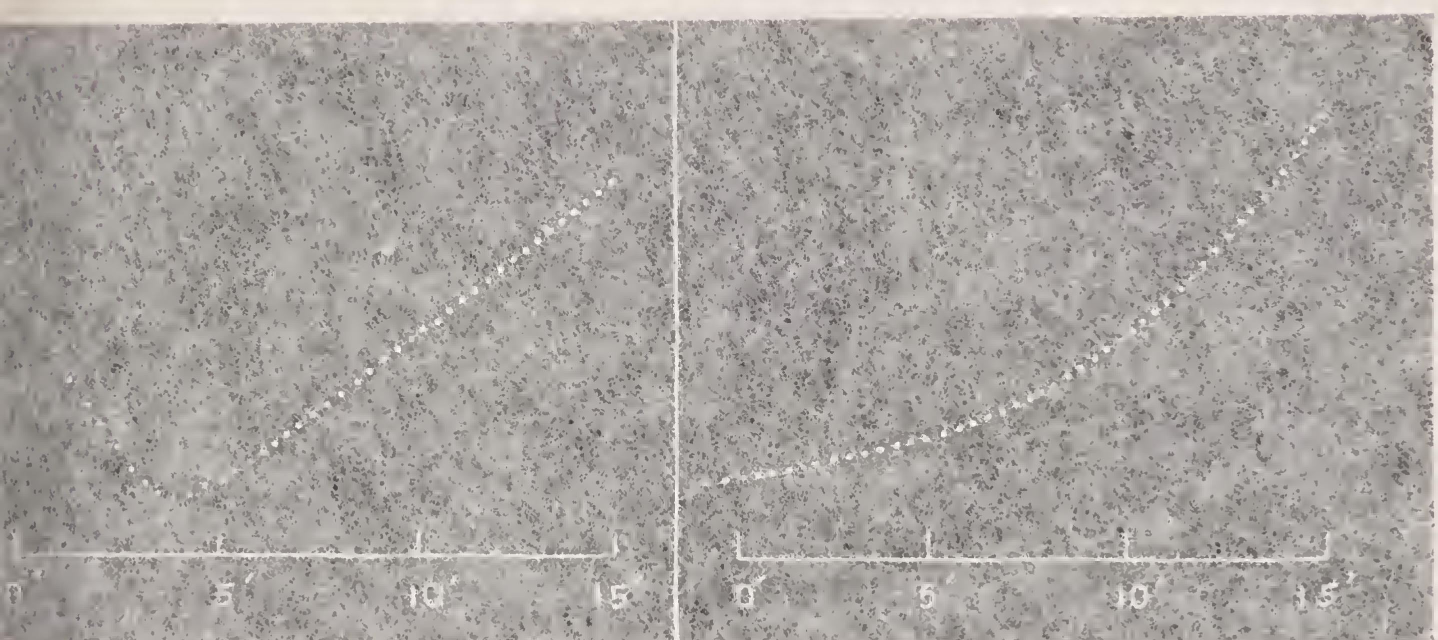


FIG. 166. FIG. 167.

FIG. 166. Geotropic response of peduncle of Tuberose; preliminary down movement is due to weight.

FIG. 167. Geotropic response of petiole of Tropaeolum; latent period shorter than 20 seconds.

Tuberose in a state of active growth; the flower itself was cut off in order to remove unnecessary weight. After a suitable period of rest for recovery from the shock of operation, the specimen was placed in a horizontal position, and its record taken. The successive dots in the curve are at intervals of 20 seconds, and the geotropic up-movement is seen to be initiated (fig. 166) after the tenth dot, the latent period being thus 3 minutes and 20 seconds, the greater part of which was spent in recovering the down-movement caused by the weight of the organ.

Experiment 156. *Geotropic response of petiole of Tropaeolum.*—I expected to obtain a shorter latent period by choosing thinner specimens with less weight. I therefore took a cut specimen of the petiole of Tropaeolum and held it at one end. The lamina was also cut off in order to reduce the considerable leverage exerted by it. The response did not now exhibit any preliminary down-movement, the geotropic up-movement being initiated within a few seconds after placing the petiole in a horizontal position (fig. 167). The successive dots in the record are at intervals of 20 seconds and the second dot already exhibited an up-movement; the latent period is therefore shorter than 20 seconds. It has been thought hitherto that the latent period for geotropic reaction is a matter of many minutes; this very high value must have been due to the crude methods employed for the determination.

The Complete Geotropic Curve

The characteristics of the geotropic curve are similar to those of other tropic curves. That is to say, the susceptibility for excitation is at first feeble; it then increases at a rapid rate; in the third stage the rate becomes uniform; and finally the curvature attains a maximum value and the organ reaches the state of geotropic equilibrium. The period of completion of the curve varies in different specimens from one to several hours.

Experiment 157.—The following record was obtained with a bud of Crinum, the successive dots being at intervals of 10 minutes. After overcoming the effect of weight (which took an hour), the curve rose at first slowly, then rapidly. The period of uniformity of movement is seen to have been attained in this case after 3 hours and continued for nearly 90 minutes. The final equilibrium was reached after a period of 8 hours (fig. 168).

For studying the effect of an external agent on geotropic reaction, the period of uniform movement is the most

suitable. Acceleration of the normal rate, with enhanced steepness of curve, then indicates that the external agent

FIG. 108. The complete geotropic curve (Crinum).

co-operates with gravity; depression of the rate with resulting flattening of the curve shows, on the other hand, the antagonistic effect of the agent.

DETERMINATION OF DIRECTION OF GEOTROPIC STIMULUS

The experiments which have been described show that it is the upper side (on which the vertical lines of force of gravity impinge) that undergoes excitation. The direction of the incident stimulus must therefore be the vertical lines of gravity. This conclusion is supported by the results of three independent lines of inquiry: (1) the algebraical

summation of the effect of geotropic with that of photic stimulation whose direction is known; (2) the relation between the directive angle and geotropic reaction; and (3) the torsional response under geotropic stimulation.

EFFECT OF ALGEBRAICAL SUMMATION

Experiment 158.—A flower-bud of Crinum is laid horizontally and a record taken of its geotropic movement. On application of light on the upper side (at L) the responsive

FIG. 169.

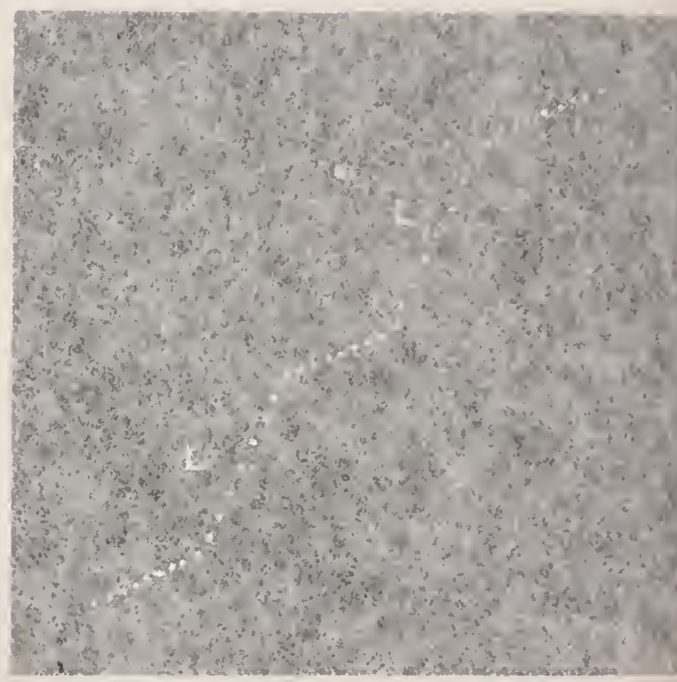


FIG. 170.

FIG. 169. Stimulus of light or gravity, represented by arrow, induces up-curvature as shown in dotted figure (Crinum).

FIG. 170. Additive effect of photic stimulus.

The first, third, and fifth parts of the curve give the normal record under geotropic stimulation. Rate of up-curvature enhanced under superposition of stimulus of light, L, acting from above.

upward curvature is enhanced, proving that gravity and light are concordant in their effects. On the cessation of light, the original rate of geotropic curvature is restored (fig. 170). Application of light of increasing intensity from below induces, on the other hand, a diminution, neutralisation, or reversal of the geotropic curvature.

Light acting vertically from above induces a concavity of the excited upper side, in consequence of which the organ moves, as it were, to meet the stimulus. The effect of geotropic stimulation is precisely similar. In fig. 169 the arrow represents the direction of stimulus which may be rays of light or vertical lines of force of gravity.

Analogy between Phototropic and Geotropic Reactions

In geotropic curvature the direction of geotropic stimulus may, for all practical purposes, be regarded as coinciding with the vertical lines of gravity. The analogy between the effects of light and of gravity is very close; [1] in both the induced curvature is such that the organ moves so as to meet the stimulus. This will be made still more evident in the investigations on torsional geotropic response described in a subsequent chapter. The tropic curve under geotropic is similar to that under photic stimulation. The tropic reaction under the stimulus both of light and of gravity increases similarly with the directive angle. These real analogies are unfortunately obscured by the use of arbitrary terminology in the description of the geotropic curvature of the shoot. The record in fig. 170 gives the response to vertical stimulation by light and by gravity of a horizontally laid bud of Crinum. In both the upper side undergoes contraction and the movement of response carries the organ upwards, so as to place it parallel to the incident stimulus. Though the reactions are similar in the two cases, yet the effect of light is termed *positive* phototropism, that of gravity *negative* geotropism. I would draw the attention of plant-physiologists to the anomalous character of the existing nomenclature. Geotropism of the shoot should, for reasons given above, be termed *positive* instead of *negative*, and it is unfortunate that long usage has given currency to terms which are misleading, and which certainly have the effect

[1] An exception to this will be found on p. 37[illegible], with an explanation.

of obscuring analogies between phenomena. Until the existing terminology is revised, it would perhaps be advisable to distinguish the geotropism of the shoot as Zenithotropism and that of the root as Nadirotropism.

Relation between the Directive Angle and Geotropic Reaction

When the main axis of the shoot is held vertical, the angle made by the surface of the organ with the lines of force of gravity is zero, and there is no geotropic reaction. The reaction increases with the directive angle; theoretically, the geotropic reaction should vary as the sine of the angle. In Chapter XXXI. I will describe the very accurate electric method which I have been able to devise for determining the relative intensities of geotropic reaction at various angles. Under perfect conditions of symmetry the intensity of reaction is found actually to vary as the sine of the directive angle.

Differential Geotropic Excitation

The geotropic excitability of a radial organ is the same on all sides. It has been shown that when it is laid horizontal it is the uppermost side that responds more effectively to the geotropic stimulation.

The two sides of a dorsiventral organ are unequally excitable to different forms of stimuli, the lower side of the pulvinus of Mimosa being far more excitable than the upper side. Since the reaction to geotropic stimulation is similar to that of other forms of stimulation, the lower side of the pulvinus should exhibit a more pronounced geotropic movement than the upper.

Under ordinary circumstances the upper half of the pulvinus is, on account of its favourable position, more effectively stimulated by gravity; in consequence of this the leaf assumes a more or less horizontal or 'dia-geotropic' position of equilibrium. But when the plant is inverted,

the more excitable lower half of the organ then occupies the favourable position for geotropic excitation. The leaf now erects itself till it becomes almost parallel to the stem (cf. fig. 179). The response of the same pulvinus which was formerly 'dia-geotropic' now becomes 'negatively geotropic', but an identical organ cannot possess two different specific sensibilities. The different effects in the two positions are in reality due to differential excitability of the two sides of the dorsiventral organ.

It has also been explained that when the pulvinus of Mimosa is subjected to lateral stimulation of any kind, it undergoes torsion, in virtue of which the less excitable half of the organ is made to face the stimulus. Experiments will be described (Chapter XXVIII) which will show that geotropic stimulation induces similar torsional response. The results obtained from this method of inquiry give independent proof (1) that the lower half of the pulvinus is geotropically the more excitable, and (2) that the direction of incident geotropic stimulus is that of the vertical lines of force of gravity which impinge on the upper side of the organ.

SUMMARY

The stimulus of gravity is shown to induce an excitatory reaction which is similar to that induced by other forms of stimulation. The immediate effect of geotropic stimulation on a horizontal growing organ is an incipient contraction and a retardation of the rate of growth of the upper side on which the stimulus is incident. This is followed by an up-curvature.

That the upper side of the stem undergoes excitatory contraction is demonstrated not only by the concave curvature of that side, but also by the excitatory reaction of galvanometric negativity of that side (p. 315).

Tropic reactions are said to be positive when the directly stimulated side undergoes contraction, with the result that

the organ curves towards the stimulus. According to this definition, the geotropic response of the stem is *positive*.

The geotropic response is delayed by the bending due to the weight of the horizontally laid shoot. Reduction of weight consequently shortens the latent period: in the case of the petiole of Tropaeolum in a highly sensitive condition, it is less than 20 seconds.

The complete geotropic curve shows characteristics which are similar to those of tropic curves in general.

A dorsiventral organ is anisotropic; the moto-excitabilities of the upper and lower sides are different. In the pulvinus of Mimosa the excitability of the lower half is greater than that of the upper half, and this differential excitability of the dorsiventral organ determines its position of geotropic equilibrium.

CHAPTER XXVII

EFFECT OF ANAESTHETICS ON GEOTROPIC RESPONSE

GEOTROPIC response of growing organs has been shown to be due to differential growth induced in the upper and lower sides of the organ, there being a retardation of growth in the directly stimulated upper side. The intensity of response will therefore depend :

1. On the normal activity of growth ;
2. On the effect of season and of various external agents which enhance or retard the normal rate of growth.

It has been shown, for instance, that growth is modified by anaesthetics in a characteristic manner. Anaesthetic agents may, according to their action, be divided into three classes :

1. Strong anaesthetics, such as chloroform, induce a preliminary acceleration of growth, followed by arrest. Continued action causes a spasmodic death-contraction.

2. Ether is less toxic than chloroform ; a small dose of ether enhances the rate of growth. It is only under prolonged application that it induces retardation or arrest.

3. Carbon dioxide is a mild anaesthetic, the immediate effect of which is an enhancement of growth. Its continuous action is followed by a decline and arrest of growth. Prolonged application often induces actual contraction.

I describe the effect of season and of various anaesthetics in modifying geotropic response.

Experimental Method

In order to obtain a characteristic response within a short time, it is desirable to choose a specimen which is sensitive and in which unnecessary weight is reduced by cutting off portions which are non-essential. These conditions are fulfilled by an isolated petiole of Tropaeolum from which the lamina has been removed. The cut ends are wrapped in moist cotton, and after a rest of about half an hour the irritability of the specimen is found to be fully restored. The beginning of the geotropic response can now be easily detected by the employment of a magnifying lever.

Tropaeolum grows in Calcutta during the winter months from November to January, and also during the spring season in February and March; the plants begin to die off from the beginning of April. The experiments described below were carried out during two years in succession. The records given by the spring and the winter-specimens exhibit certain characteristic differences. In the spring-specimen the latent period—the time which elapses between the application of the stimulus of gravity and the commencement of the geotropic up-movement—varies from 20 seconds to 6 minutes; the rate of movement afterwards becomes uniform and remains so for about half an hour. The slope of the curve and the distance between the successive dots indicate the geotropic activity; any induced enhancement of the normal rate is, as already explained, exhibited by the erection of the curve and greater separation of the successive dots; depression, on the other hand, is indicated by the opposite change. In the winter-specimen, owing to the general depressed rate of growth, the geotropic response is very sluggish, as seen in the prolonged latent period, which in the particular experiment was found to be 48 minutes; the sluggish character of the response is also indicated by the gentle slope of the geotropic curve (fig. 171).

The uniformity of the erectile response cannot be main-

tained for an indefinite period, since any further response is impossible after the full erection of the organ. It is therefore more practical to begin with it a few degrees below the horizon, and continue the record till it rises to

FIG. 171.—Geotropic curves: (*a*) of a spring-, and (*b*) of a winter-specimen. The latent period of the former is in the present case 6 minutes, of the latter 48 minutes.

Note the relatively erect curve of the spring-specimen, indicating a more intense geotropic reaction (Tropaeolum).

Time-interval between dots 3 minutes.

the same angle above the horizontal position. The slope of the curve is then found to remain practically uniform for about half an hour, which is more than sufficient for the completion of an experiment on the action of the anaesthetic. The effect of anaesthetics will be described not only on the growing but also on the pulvinated organ.

Effect of Chloroform on Geotropic Response of Growing Organs

The following experiments on the action of chloroform were carried out with two different species of plants with the object of bringing out certain characteristic differences.

Fig. 172. Effect of chloroform on geotropic response. *a*, enhancement of geotropic reaction in Eclipta; *b*, preliminary enhancement followed by arrest in Tropaeolum (*see* text).

Experiment 159. *Seedling of Eclipta.*—The epidermis of Eclipta is somewhat impervious to vapour; hence a relatively small quantity of chloroform vapour is absorbed by the plant. The characteristic effect is seen to be a great enhancement of geotropic reaction which persisted for a considerable length of time (fig. 172, *a*). The moment of application of the anaesthetic is indicated by an arrow.

Experiment 160. *Petiole of Tropaeolum.*—In the last experiment absorption of a small quantity of chloroform

gave rise to acceleration, which is characteristic of the first stage. In Tropaeolum the petiole absorbs the vapour more readily, consequently the enhancement of geotropic reaction at the first stage is followed by an arrest at the second stage (fig. 172, *b*).

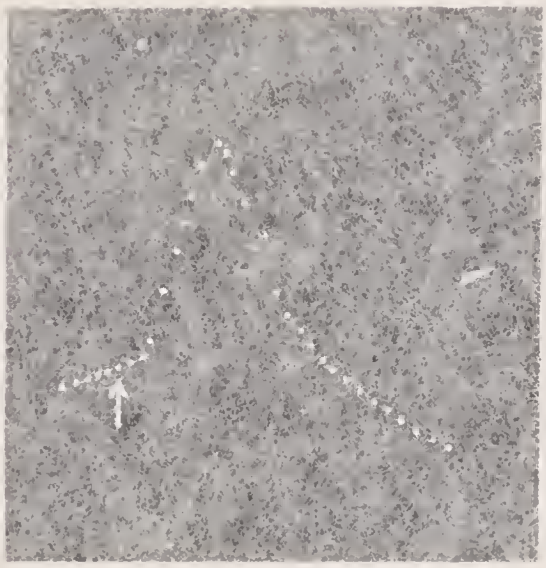


FIG. 173. Effect of chloroform on geotropic response of the terminal leaflet of Desmodium.

Note enhancement at the first and reversal at final stage

Experiment 161. *Effect on pulvinus of terminal leaflet of Desmodium.*—The leaflet was executing a slow up-movement. Application of chloroform induced preliminary enhancement of geotropic reaction in the course of 40 seconds. Continued action induced a reversal of the geotropic movement (fig. 173).

EFFECT OF ETHER ON GEOTROPIC CURVATURE

Experiment 162. *Petiole of Tropaeolum.*—After the attainment of uniform geotropic up-movement, a specimen of Tropaeolum was subjected to the action of ether vapour; this induced a great enhancement of the movement in the course of 3 minutes, as seen in the erection of the curve and its wider spacing of the successive dots (fig. 174).

Having thus obtained a definite proof of the enhancement

of the geotropic reaction under ether two batches of six similar petioles of Tropaeolum were taken and placed horizontally; of these, the first batch was placed in a chamber containing air, the second batch being placed in a chamber which contained a small quantity of ether vapour. On examining the two batches after an hour, it

FIG. 174. Effect of ether in enhancing geotropic response (petiole of Tropaeolum).

was found that while a slight curvature was produced in the specimens under normal conditions, those subjected to vapour of ether had become highly erected, the tips being even bent backwards. The striking difference between the two will be seen in the reproduction from a photograph of the normal and the etherised specimens (fig. 175). The experiments on pulvinated and on growing organs thus exhibit similar results—namely, an enhancement of geotropic reaction under moderate application of ether

vapour. I next describe the effect of the mild narcotic carbonic acid gas on geotropic response.

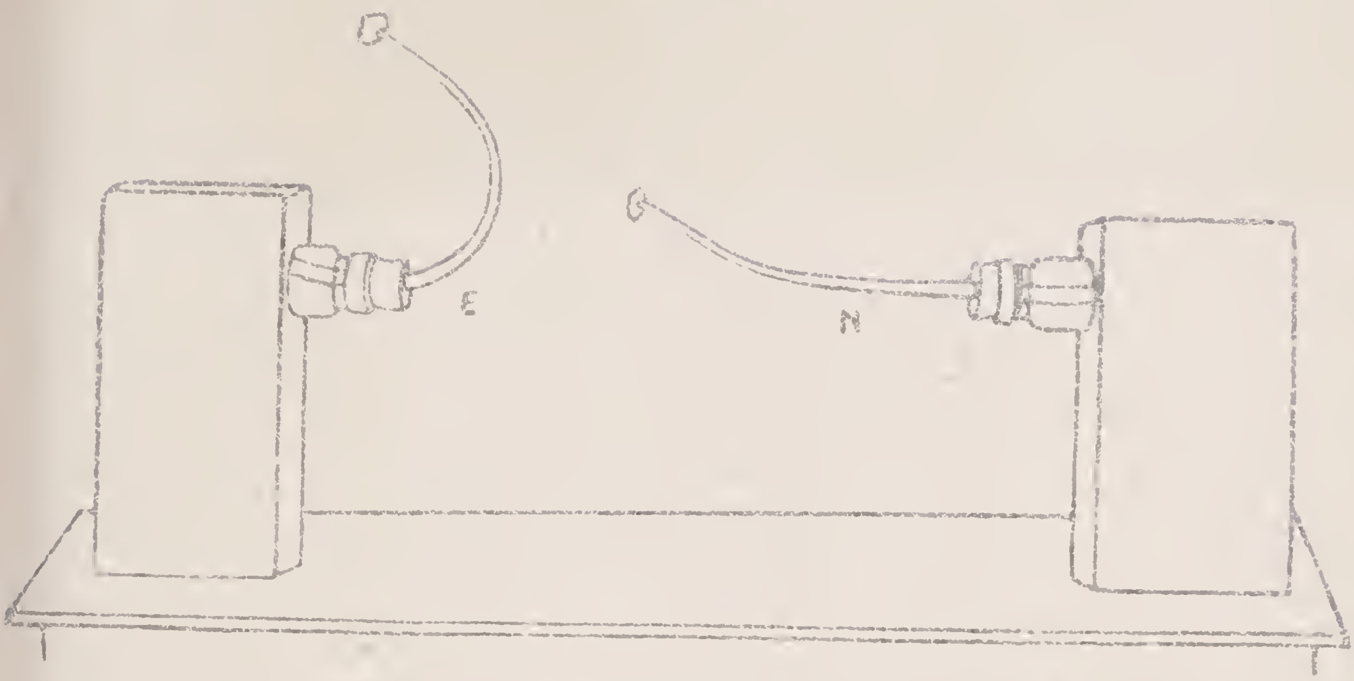


FIG. 175. Effect of ether vapour on geotropism. N, the normal reaction in air; E, the reaction in an atmosphere of ether vapour.

EFFECT OF CARBONIC ACID GAS ON GEOTROPIC RESPONSE OF GROWING ORGANS

It has been explained that the intensity of geotropic response is to a certain extent modified by the season. I describe effects of application of CO_2 to winter- and to spring-specimens.

Experiment 163. *Effect of CO_2 on winter-specimen of Tropaeolum.*—The record given (fig. 176) shows the sluggishness of response in the cold season. The latent period was found to be 40 minutes (first part of the record not shown in the figure). A geotropic curvature was then initiated at a slow rate, as seen in the slightly inclined curve of ascent. Carbonic acid gas was next passed into the plant-chamber; this caused a great enhancement of the geotropic reaction in the course of about 3 minutes. The induced enhancement is clearly seen in the very erect curve, and in the separation of the successive dots; the acceleration persisted for 20 minutes, after which the movement became

arrested. This arrest was not permanent, for introduction of fresh air was found to bring about the subsequent renewal of the geotropic up-movement.

Experiment 164. *Response of spring-specimen.*—The record (fig. 177) shows that the latent period is relatively

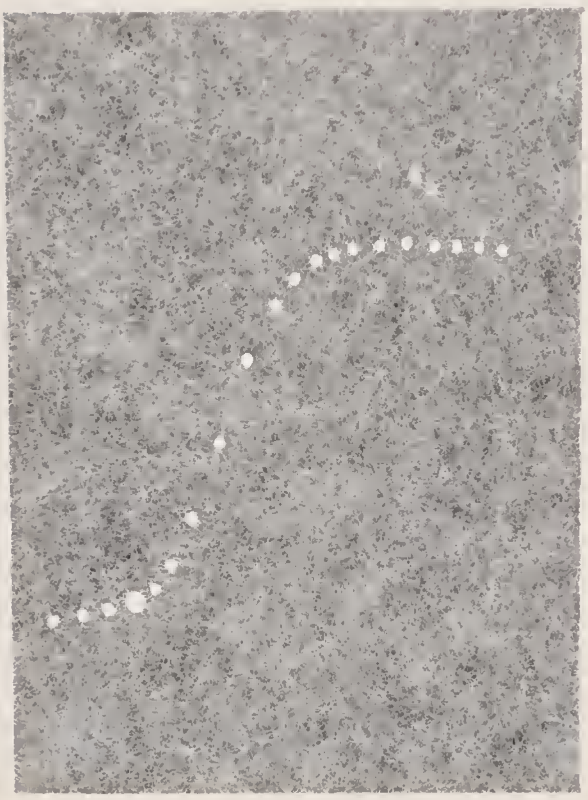


FIG. 176.

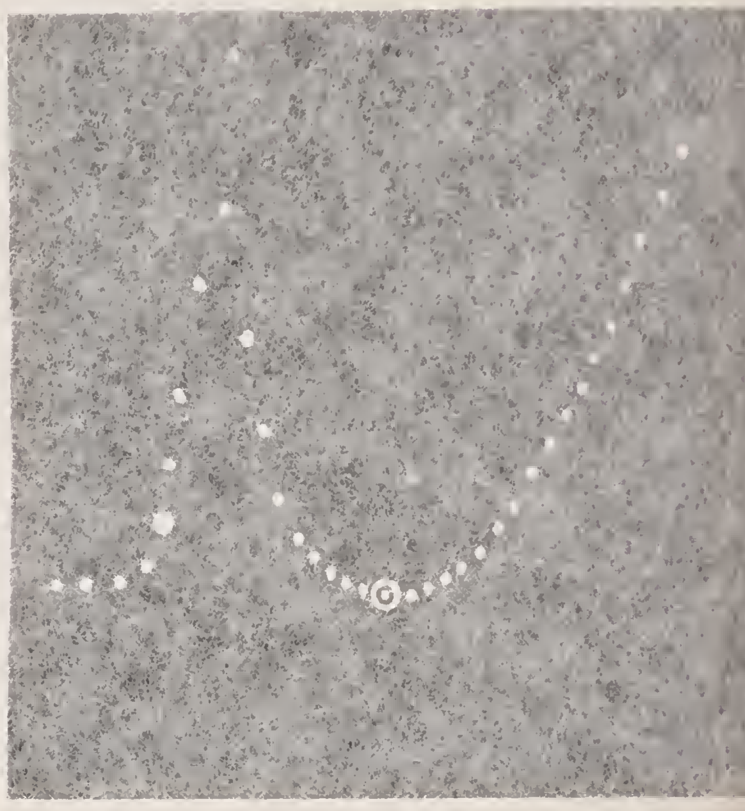


FIG. 177.

FIG. 176. Effect of CO_2 on geotropic response of winter specimen of Tropaeolum. CO_2 applied at thick dot induced preliminary enhancement followed by arrest.

Successive dot-intervals 3 minutes.

FIG. 177. Effect of CO_2 on geotropic response of spring-specimen of Tropaeolum. CO_2 applied at thick dot and fresh air substituted at circle. The effect induced is a preliminary enhancement followed by a reversal. Substitution of fresh air renewed normal geotropic reaction.

short; the erect curve, moreover, demonstrates greater geotropic sensibility of the spring-specimen. After the attainment of a uniform erectile movement, carbonic acid gas was introduced into the plant-chamber; this induced a great enhancement of geotropic movement in the course of 3 minutes, a result characteristic of the first stage. The erectile movement was temporarily arrested in the course of 12 minutes. There then followed *the reversal of the*

normal geotropic movement which carried the tip of the specimen below the horizontal position. Carbonic acid gas thus caused an apparent reversal of normal geotropic response. Fresh air was then introduced in the chamber, with the result that the normal geotropic up-movement was renewed after an interval of 5 minutes.

In another experiment a stream of carbonic acid gas was maintained throughout, the experiment lasting for more

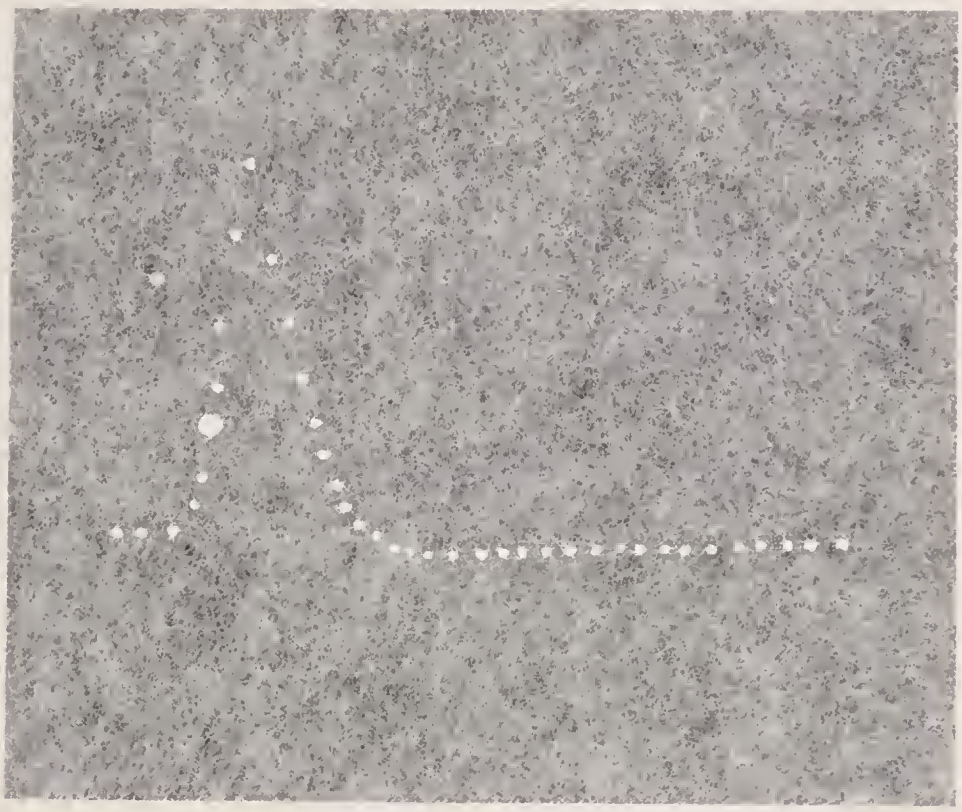


FIG. 178. Effect of CO_2 on geotropic response of Tropaeolum. Enhancement of geotropic response followed by persistent reversal under continued action of the gas

than an hour. It gave the same sequence of effects as before—namely, enhancement at the first stage, a temporary arrest at the second, and an actual reversal at the third stage (fig. 178). The tip of the specimen under the continued action of gas persisted in its reversed position.

The results described above relate to the action of carbonic acid gas on the geotropic response of Tropaeolum. In order to demonstrate the universality of the phenomenon, further investigations were undertaken with a large number of growing and of pulvinated organs.

Experiment 165. *Response of the peduncle of Tuberose.*—This specimen gave a normal geotropic response, though it was relatively sluggish. The latent period was 15 minutes. The effect of CO_2 was a preliminary enhancement, followed by arrest and reversal of normal geotropic response. On the substitution of fresh air in the plant-chamber, the normal up-movement was once more restored. Continued action of carbon dioxide is thus seen to produce in the Tuberose a reversal of geotropic action similar to that observed in Tropaeolum.[1]

In regard to the reversal of geotropic movement under carbon dioxide, it is to be borne in mind that geotropic response is ultimately due to induced variation in the rate of growth. It has been shown that all narcotics, including carbonic acid gas, ether, and chloroform, induce variation in the rate of growth, an acceleration at the first stage, an arrest at the second, and a reversed contractile response at the third stage. Corresponding to these are the acceleration, arrest, and reversal of geotropic movement. The effect of CO_2 is therefore by no means unique, but the common reaction under all narcotic agents.

Effect of Carbonic Acid Gas on Geotropic Response of Pulvinated Organ

The geotropic excitability of the upper half of the pulvinus of Mimosa, as previously explained, is very much less than that of the lower half. It thus happens that the leaf of Mimosa is in a state of equilibrium in a horizontal, the so-called dia-geotropic, position. But if the plant be inverted so that the relatively more excitable lower half is above, the geotropic excitation and the resulting curvature are greatly enhanced, the leaf becoming continuously erected in this inverted position. The experiment may be

[1] J. Lynn observed (*New Phytologist*, Aug. 19, 1921) a reversal of geotropic curvature in the hypocotyl of *Helianthus annuus* under the action of carbonic acid gas. He suggests in explanation a far-fetched theory of hydrion concentration, for which no experimental verification has been adduced.

carried out with a small piece of a shoot of Mimosa bearing a lateral leaf; the sub-petioles may also be cut off, thus reducing the weight of the organ. In order to prevent drying, the cut ends of the stem and of the petiole are covered with small pieces of moist cloth. The sensibility of the pulvinus is fully restored in the course of an hour, as shown by the normal fall of the petiole under mechanical stimulation. The advantage of a cut specimen is that it can be easily manipulated and held in the inverted position (fig. 179).

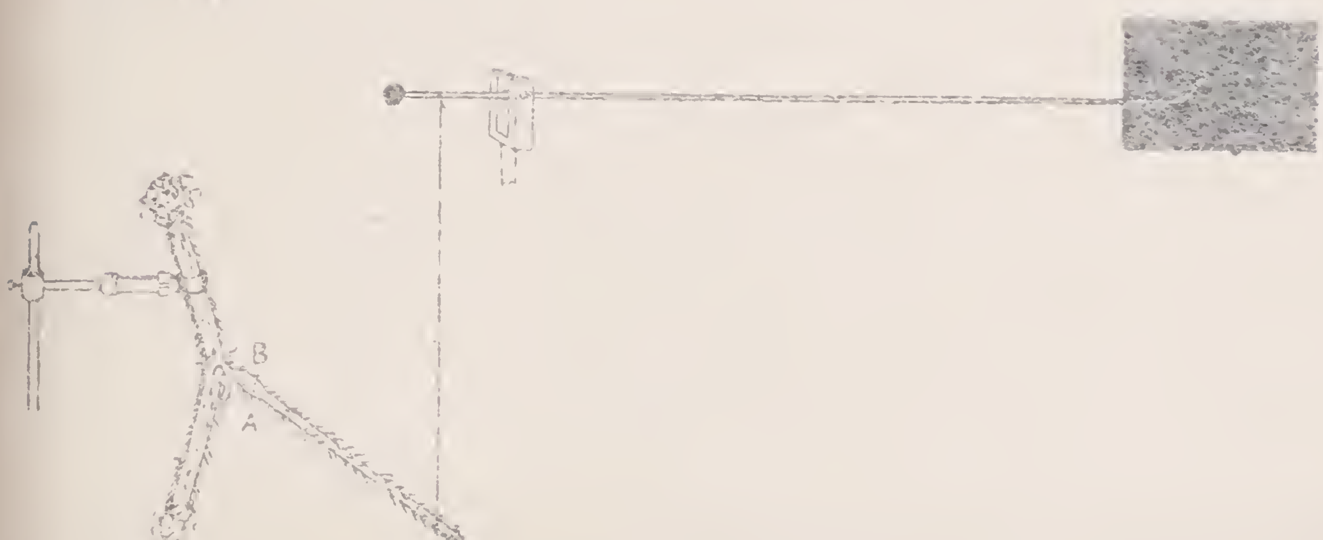


FIG. 179. Method of record of geotropic response of Mimosa held in an inverted position with the more excitable half of pulvinus B facing upwards.

Experiment 166. *Effect of CO_2 on geotropic response of Mimosa.*—The first part of the record in fig. 180 shows the uniform erectile geotropic response in the inverted position. The plant-chamber was next filled with carbon dioxide. This caused an arrest and a subsequent reversal of the geotropic response, which occurred 2 minutes after the application of the gas. *By this reversal the leaf was brought below its original position and maintained there.* Substitution of fresh air brought about a restoration, and normal geotropic response was renewed in the course of 4 minutes.

Experiment 167. *Erythrina indica.*—The pulvinus of Erythrina is less sensitive than that of Mimosa; the characteristic effects are, in other respects, the same in the two

cases. The cut specimen was held in an inverted position, and after the attainment of uniform up-movement, carbonic acid gas was applied; this caused a reversal of the normal geotropic movement in the course of 4 minutes and 20 seconds; the petiole was thus lowered below its original position. Introduction of fresh air gave rise, in the course

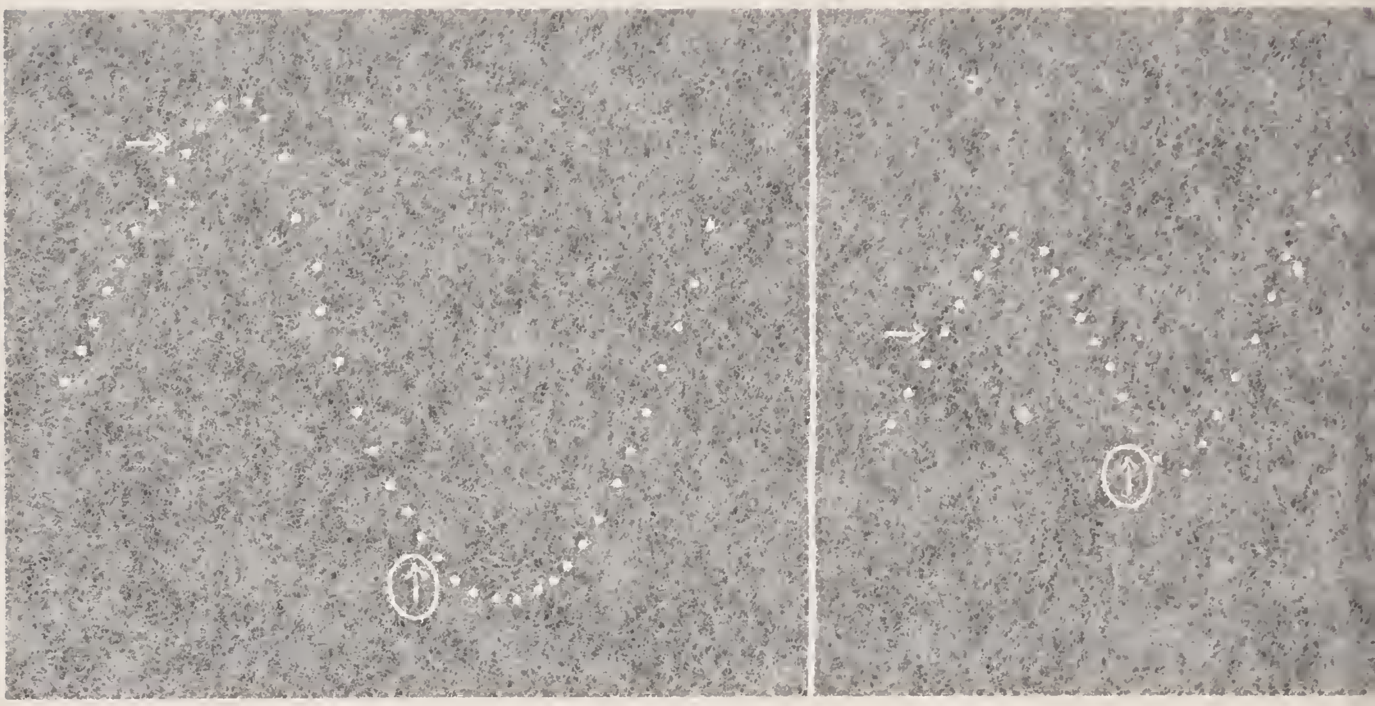


Fig. 180. Fig. 181.

Fig. 180. Effect of CO_2 on geotropic response of Mimosa applied at arrow; second arrow within a circle represents substitution of fresh air.

Successive dots at intervals of a minute.

Fig. 181. Effect of CO_2 on geotropic response of Erythrina indica. Note actual reversal of geotropic response under CO_2.

of 2 minutes, to the renewal of normal erectile movement (fig. 181).

Results obtained with various growing and pulvinated organs thus show that the normal geotropic response is reversed under the continued action of carbonic acid gas. The effect of CO_2 in reversal of geotropic response is by no means unique, for it occurs under the action of other anaesthetics as well. The period of application of the anaesthetic for reversal is relatively shorter in the case of strong anaesthetic like chloroform, but the fundamental reaction is similar in all cases.

Summary

The geotropic reaction of a growing organ is dependent on its growth-activity. In spring the latent period is relatively short and the rate of erectile movement rapid. In winter the latent period is prolonged and the geotropic movement is very sluggish.

The effect of chloroform in moderate dose is an enhancement of geotropic reaction followed by arrest. Stronger application produces a reversal.

Ether, in moderate dose, induces a very marked enhancement of geotropic reaction, the organ becoming fully erected in a short time. The geotropic response of pulvinated organs is also greatly enhanced under moderate application of ether.

The immediate effect of carbonic acid gas on geotropic response of both growing and pulvinated organs is an enhancement of the erectile movement above the normal. Continued action of CO_2 gives rise to a reversal of the normal geotropic movement.

CHAPTER XXVIII

GEOTROPIC TORSION

I HAVE explained that lateral application of certain stimuli to the flanks of a dorsiventral organ induces a responsive torsion by which the less excitable side is made to face the stimulus (p. 256). I now show that the reaction to the

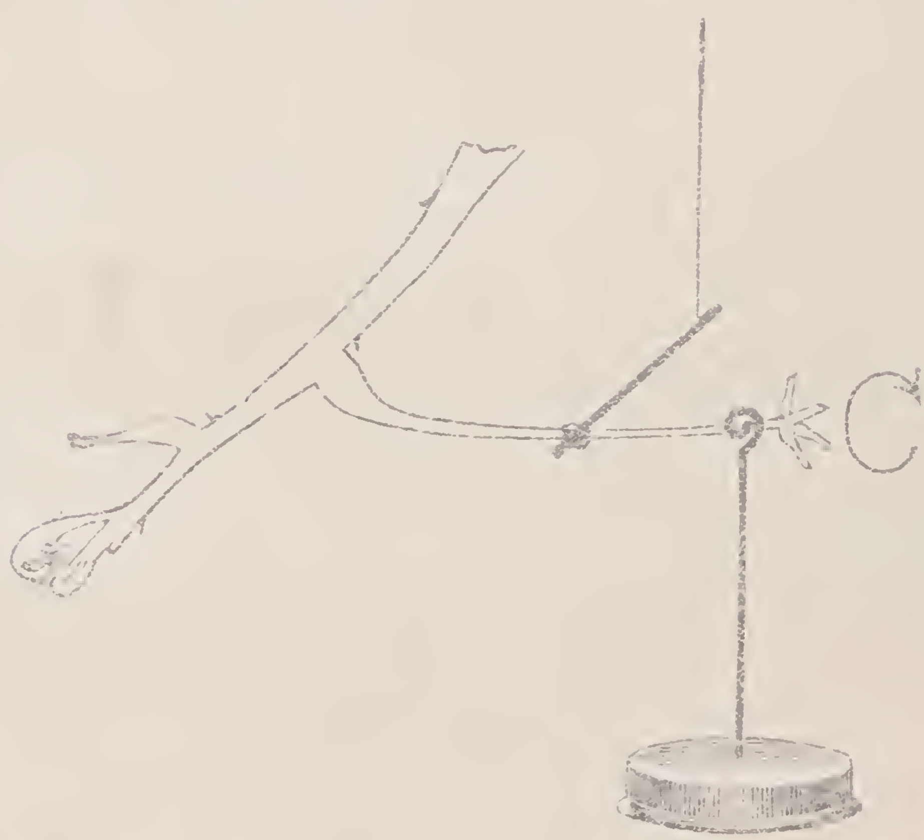


FIG. 182. Diagram of arrangement for recording torsional response of leaf of Mimosa to geotropic stimulation. The less excitable upper half of the pulvinus is to the left.

stimulus of gravity is in every respect similar to that to other forms of stimulation.

As the direction of force of gravity is fixed, it is necessary that the dorsiventral organ should be movable, that it may be so placed that the geotropic stimulus may act upon its

flank. In the following experiments the pulvinus of Mimosa was taken as the typical dorsiventral organ. For lateral stimulation, the plant is placed on its side, so that the vertical lines of gravity impinge on one of the two flanks of the organ. Two different positions, *a* and *b*, are distinguishable. In the *a* position the apex of the stem and the upper half of the pulvinus are to the left of the observer, and in the *b* position they are to the right. The arrangement for taking a record of the torsional response in the *a* position is shown in fig. 182.

Torsional Response under Geotropic Stimulation

Experiment 168. *Torsional response.*—When the leaf is in *a* position, the geotropic torsion is in the direction of the

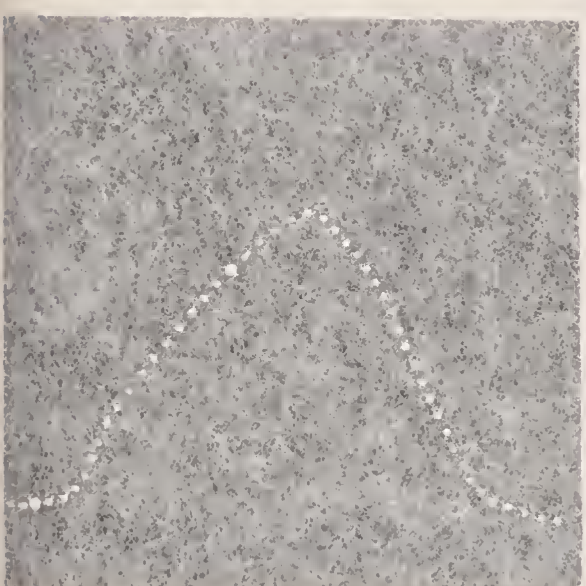


Fig. 183.

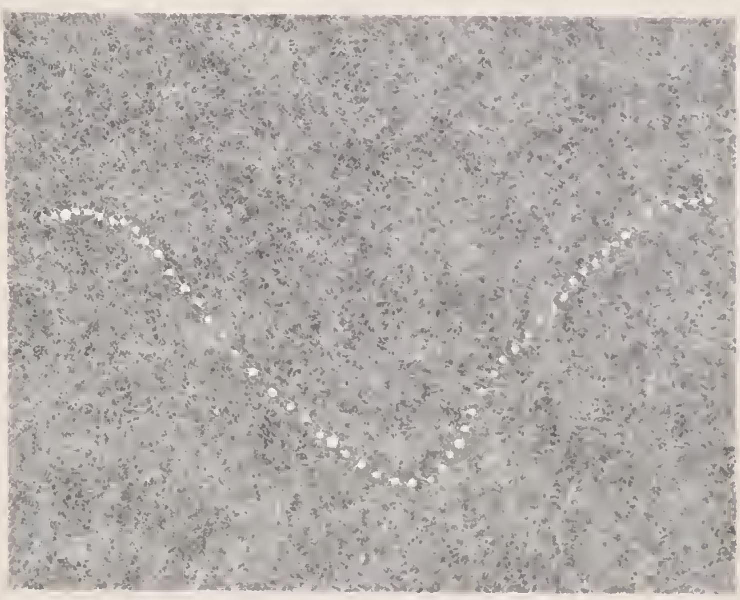


Fig. 184.

Fig. 183. Torsional response under geotropic stimulation. Clockwise torsion in *a* position is shown in the record as an up curve. (Mimosa.)

Fig. 184. Anti-clockwise torsion in *b* position shown in the record as down-curve.

In both these records there is a recovery on restoration of the pulvinus to the normal position. The interval between two thick dots represents duration of stimulation.

movement of the hands of the clock. The clockwise torsion induced is indicated in the record (fig. 183) as an up-curve;

on restoration of the pulvinus to the normal position there is a recovery shown by the down-curve.

Experiment 169. *Anti-clockwise torsion in b position.*—The experiment was repeated with this difference, that the opposite flank was now exposed to the vertical lines of force of gravity. The record (fig. 184) shows by the down-curve the anti-clockwise movement, and subsequent recovery on removal of stimulation.

It has already been explained that the direction of incident stimulus can be found from the responsive torsion by which *the less excitable side of the organ is made to face the stimulus.* The results of experiments just described prove conclusively that the direction of geotropic stimulus must be the vertical lines of force of gravity—a conclusion which is of great theoretical importance.

Algebraical Summation of Geotropic and Phototropic Effects

Experiment 170.—If the direction of the incident geotropic stimulus is vertical, and should the leaf be in the *a* position, then the stimulus of light acting from above should enhance the previous torsional response due to geotropism. In the above case the directions of the lines of gravity and of the rays of light coincide. The effect of rays of light acting from below should, on the other hand, oppose that of gravity. The additive effect of stimulation by both light and gravity is seen in the record (fig. 185). The first part of the curve is the record of pure geotropic torsional movement. Light from above is applied at L; the rate of movement is seen to have become greatly accelerated. On cutting off the light the enhanced rate induced by it is found to disappear, the response curve being now solely that of geotropic reaction. The effect of phototropism in opposition to geotropism is demonstrated by the following experiments, where the opposing action of light of different

intensities gives rise to a partial balance, to an exact balance, or to an overbalance.

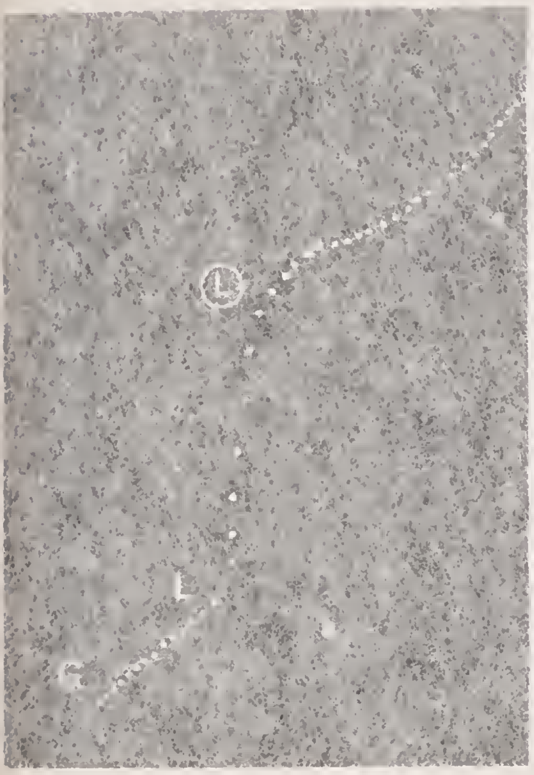


FIG. 185.

FIG. 186.

FIG. 185. Additive effect of stimulation by gravity G, and by light L. Application of light at L increases torsional response. Removal of light (L in circle) restores original geotropic torsion.

FIG. 186. Algebraical summation of geotropic and phototropic action. Light applied below at –L opposes geotropic action. Cessation of light (–L within a circle) restores geotropic torsion.

BALANCE OF GEOTROPIC BY PHOTOTROPIC REACTION

Experiment 171. *Photo-Geotropic Balance.*—I describe in detail the procedure for obtaining an exact balance. A parallel beam of light from a small arc-lamp is reflected by means of an inclined mirror, so as to act on the junction of upper and lower halves of the pulvinus from below. An iris-diaphragm regulates the intensity of incident light. The first part of the curve is the record of normal geotropic torsional movement. Light of a given intensity was applied from below at a point marked –L (fig. 186); this is seen to produce an overbalance, the phototropic effect being slightly in excess. The intensity of the incident light was

continuously diminished by regulation of the diaphragm till exact balance was obtained, as shown by the horizontal part of the record. It is with great surprise that one comes to realise the fact that the effect of one form of stimulus can be so exactly balanced by that of another entirely different, and that the stimulus of gravity can be measured, as it were, in candle powers of light! After securing the balance, light was cut off, and geotropic torsion was renewed on the cessation of the counteracting phototropic reaction.

Experiment 172. *Comparative balancing effects of white and red light.*—White light was at first applied at −L in opposition to the geotropic movement. The intensity of light was stronger than was necessary for exact balance, and its effect was at first to retard and then to reverse the torsional geotropic response. When thus overbalanced, a red glass was interposed in the path of the light at R. As the phototropic effect of this light is comparatively feeble, the geotropic torsion became predominant, as seen in the subsequent up-curve. The red glass was then removed, white light being substituted at −L to stimulate once more in opposition; the result is seen in the final overbalance, and reversal of torsion (fig. 187).

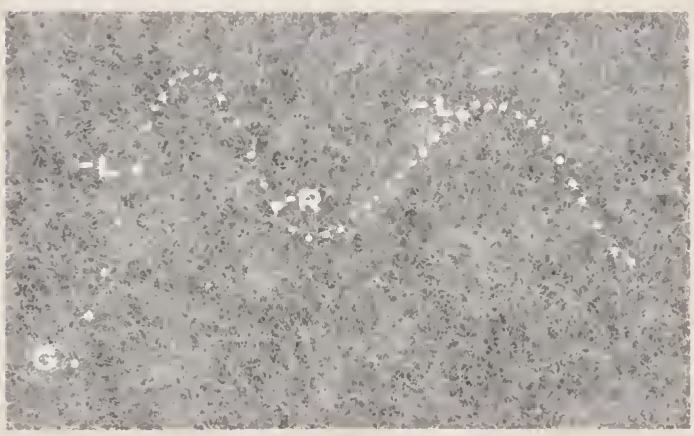


FIG. 187. Application of white light at −L in opposition causes reversal of torsion. Red light, R, is ineffective, and geotropic torsion is restored. Reapplication of white light causes once more the reversal of torsion.

Experiment 173. *Effect of coal-gas on the balance.*—The method of balance described above opens out new possibilities in regard to investigations on the relative modifications of geotropic and phototropic excitability by any given external change. Traces of coal-gas are known to enhance the phototropic excitability of an organ, while continued absence of oxygen is found to depress it. The experiment

I am going to describe shows (1) the enhancement of phototropic excitability on the introduction of coal-gas, and (2) the depressing effect of excess of coal-gas in depriving the organ of its supply of oxygen. After taking the normal curve of geotropic torsion, light was applied below at −L and an exact balance obtained in the course of 2 minutes, as seen in the top of the curve becoming horizontal. Coal-gas was now introduced into the plant-chamber at C. This induced an enhancement of phototropic reaction with resulting overbalance shown by the reversal of torsion. This enhancement persisted for more than 3 minutes. By this time the plant-chamber was completely filled with coal-gas, and the resulting effect on the phototropic reaction is seen in the second upset of the balance, this time to be depression (fig. 188). It would seem that the cells which respond to light are situated nearer the surface of the organ than those which react to geotropic stimulus. Hence an agent which acts on the organ from outside induces phototropic change earlier than geotropic.

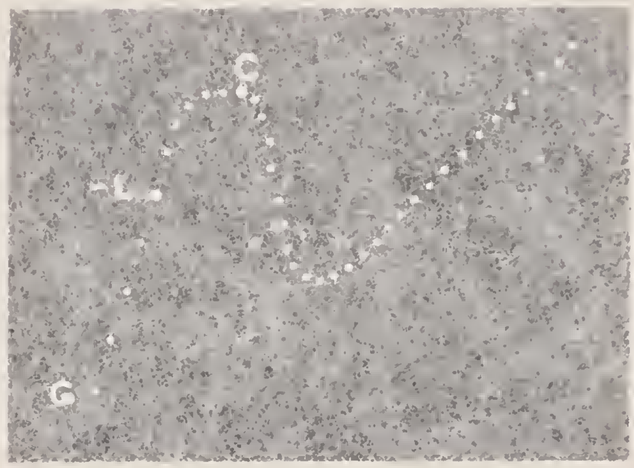


FIG. 188. Effect of coal-gas on photo-geotropic balance. Geotropic torsion, G, is exactly balanced by opposing action of light, −L. Application of coal-gas at C at first caused enhancement of phototropic reaction with resulting reversal. Prolonged application induced depression of phototropic reaction, the geotropic effect thus becoming predominant.

SUMMARY

Under lateral action of geotropic stimulus, a dorsiventral organ exhibits a torsional response such that the less excitable half of the organ is made to face the stimulus.

The direction of incident geotropic stimulus is the same as the direction of the vertical lines of gravity.

It is the upper side of the organ that is directly stimulated by geotropic action.

The effects of gravity and of light are algebraically summated when in simultaneous action. Light may be made to act in opposition to the stimulus of gravity. By suitable adjustment of the intensity of light, the two torsions can be exactly balanced.

This state of balance is upset by any slight variation in the intensity of the opposing photic stimulation.

The relative modification of geotropic and phototropic reaction by an external agent can be determined by the resulting upset of the Photo-Geotropic Balance.

CHAPTER XXIX

THE GEO-ELECTRIC RESPONSE OF THE SHOOT

Having described the geotropic response and its modification under variation of external conditions, the question arises as to the underlying mechanism by which stimulation is effected. The only conceivable way in which gravity can produce stimulation in the higher plants is by the pressure of weight acting on the sensitive ectoplasm of the cells. The pressure of weight can be exerted by the cell-contents, whether the sap, or the heavy particles, crystals or starch-grains, contained in the cell. The former, the Theory of Hydrostatic Pressure, was suggested by Pfeffer and supported by Czapek; the other, the Theory of Statoliths, has been advocated by Noll, Haberlandt, and Němec.

In the case of a multicellular stem laid horizontally, E and E′ as indicated in the diagram (fig. 180) may be regarded as the tissue in the cells of which stimulation is caused by the pressure of particles. It is to be noted that in the sensitive cells of the upper half the pressure is exerted on the inner tangential protoplasmic layer, while in the lower half the pressure is exerted on the outer ectoplasmic layer. Facts will be described which indicate that the protoplasmic layer is not equally excitable on all sides of the cell, which may possibly offer an explanation of the opposite reactions on the two sides of the organ, the upper exhibiting excitatory contraction, while the lower exhibits the opposite reaction of expansion.

Having discovered that all excitatory contractions in plant-tissues can be detected by the induced galvanometric

negativity. I have been working for many years to find an independent means of recording the effect of geotropic stimulation by means of electric response. The characteristic electric record is modified, as is the mechanical record, by the bending down of the stem which precedes the geotropic up-movement. I was able to eliminate this complicating factor by restraining all movement of the shoot, the responsive change of galvanometric negativity being an independent expression of excitatory reaction. The following account is quoted from my previous work published in 1907:[1]

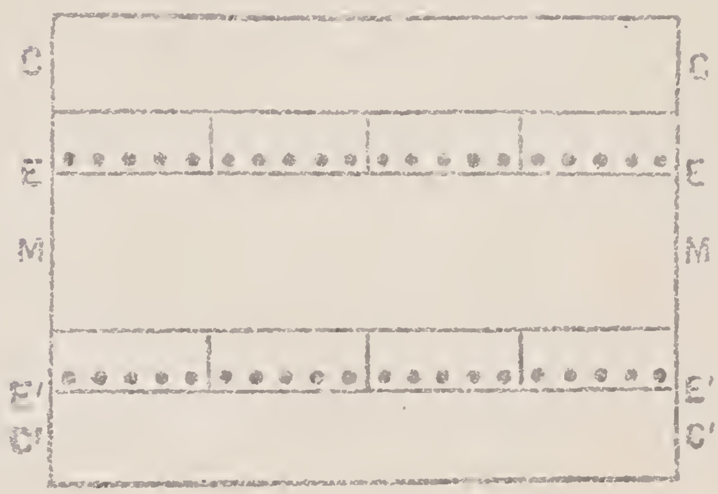


FIG. 189. Diagrammatic representation of a multicellular organ laid horizontally and exposed to geotropic stimulation.

In the upper half, the statoliths act on the protoplasm lining the inner side of the tangential wall E; in the lower half they act on the protoplasm lining the outer side of the tangential wall of E'. (After Francis Darwin.)

'The secondary effect, due to mechanical disturbance, which masks for a time the excitatory effect of gravitational stimulus, may thus be eliminated completely by restraining all movement of the shoots. The problem thus resolves itself into the fixing of an experimental shoot—say, the peduncle of Eucharis Lily—in such a way that mechanical response is completely restrained. The next point is to subject the specimen at a given moment to the stimulus of gravity, and to record the consequent electric response.

'It is clear that when any two points are acted on symmetrically by the force of gravity, there is no resultant geotropic action. This is the case in regard to two diametrically opposite points A and B situated laterally on an erect shoot. When the shoot is laid horizontally, two lateral points are likewise acted on symmetrically by the force of

[1] *Comparative Electro-Physiology*, p. 414.

gravity, and there is thus no *differential action* as between the two. But if the shoot be now rotated on itself, so that one of these points is diametrically above and the other below, a differential effect will be induced between the upper and lower sides, the upper being the more excited. In the following experiment I took a specimen of Eucharis Lily, and fixed the entire plant horizontally (fig. 190). The pivoted support allowed the responsive points A and B to be at first lateral.

'Owing to symmetry there was now no differential action of gravity, nor any consequent electric variation

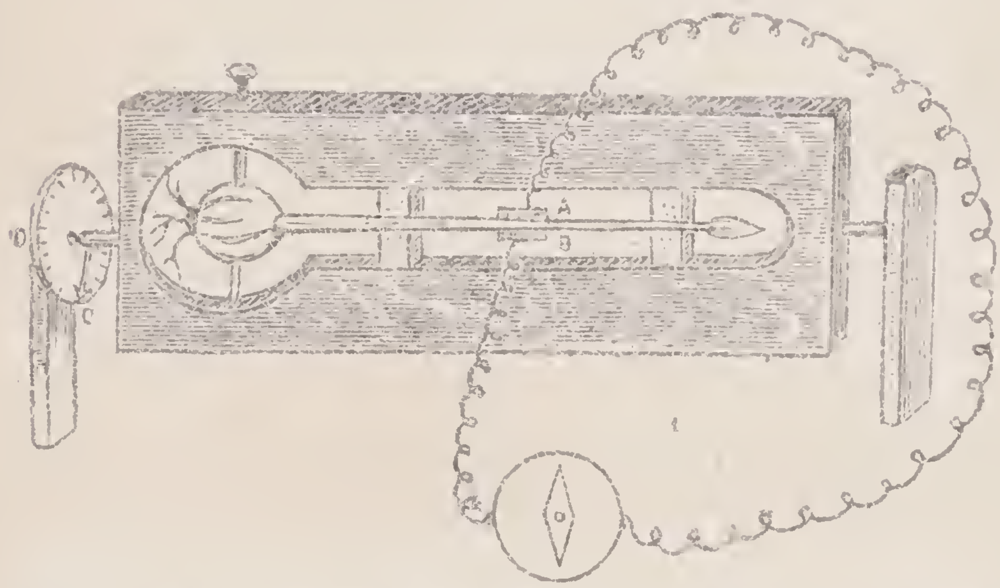


FIG. 190. Experimental arrangement for subjecting the shoot to geotropic stimulation, mechanical response being restrained.

between the two. The specimen on its support was next quickly rotated through 90°. An electric response was perceived in about one minute, which went on augmenting with time, the upper side being increasingly galvanometrically negative. By now rotating the specimen back through 90°, the action of gravity is virtually removed. The after-effect persists for two minutes, and after this the response-curve shows the usual recovery' (fig. 191).

Experiment 174.—I repeated the experiment by the above method with *Polianthes tuberosa*, first by rotating through 90° so that A was above. This gave the up-response of galvanometric negativity of that side, which disappeared on return to 0°. The rotation was next carried through

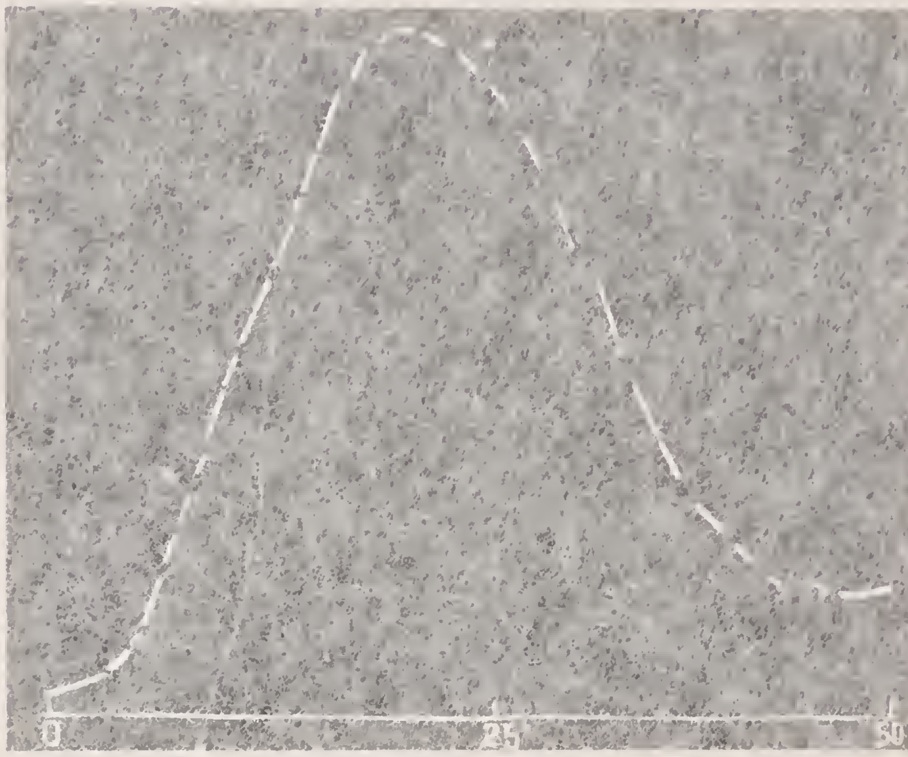


FIG. 101. Geo-electric response of the physically restrained scape of Eucharis Lily.

Up-curve represents responsive current from upper to lower surface during action of geotropic stimulus. Down curve represents recovery on cessation of stimulation. Response commenced after latent period of 1 minute; after-effect persisted for 2 minutes. Breaks in curve are due to obscuration of recording spot of light at brief intervals.

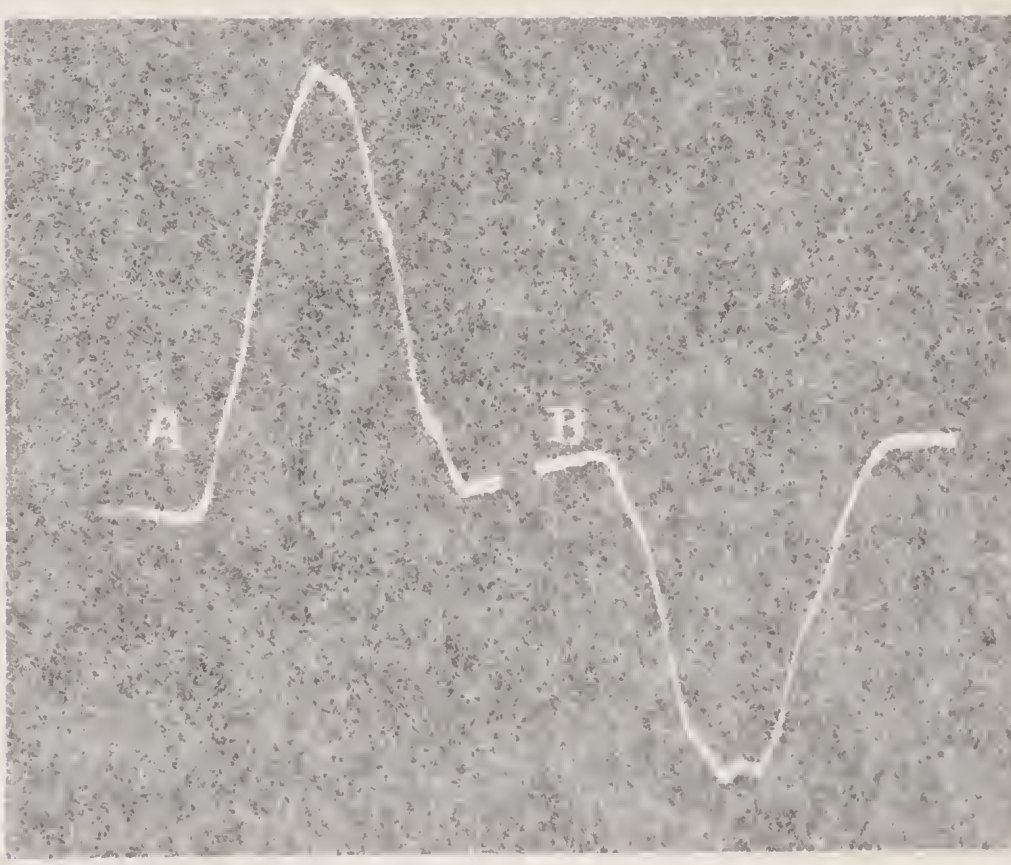


FIG. 102. Successive responses, first A above and secondly B above (Polianthes tuberosa).

$-90°$, the side B being now the upper; the induced galvanometric negativity of that side gave down-response which disappeared on return to the zero position (fig. 192).

Experimental Arrangement

I give a more detailed account of the experimental method. The sensitiveness of the galvanometer for the record should be such that a current of 10^{-10} amp. gives a deflection of 1 mm. at a distance of a metre.

Non-polarisable electrodes.—The electric connections with the plant are usually made by means of non-polarisable electrodes (amalgamated zinc rod in zinc-sulphate solution and kaolin paste with normal saline). I at first used this method and obtained all the results which will be presently described. But the employment of the usual non polarisable electrodes with liquid electrolyte is, for the present purpose, extremely inconvenient in practice; for the plant-holder with the electrodes has to be rotated from vertical to horizontal through 90°. The reliability of the non-polarisable electrode, moreover, is not above criticism. The zinc-sulphate solution percolates through the kaolin paste and ultimately comes in contact with the plant, seriously affecting its excitability. The term 'non-polarisable electrode' is in reality a misnomer; for the action-current (whose polarising effect is to be guarded against) is excessively feeble, being of the order of a millionth of an ampere or even less; the counter-polarisation induced by such a feeble current is practically negligible.

The idea that non-polarisable electrodes are meant to get rid of polarisation is thus not justified by the facts of the case. The real reason for its use is very different. The electric connection with the plant has to be made ultimately by means of two metal contacts. If two pieces of metal even from the same sheet be taken and put in connection with the plant, a voltaic couple is produced owing to slight physical differences between the two electrodes

Amalgamation of two zinc rods with mercury reduces the electric difference, but cannot altogether eliminate it.

I have been able to wipe out the difference of potential between two pieces of the same metal, say, of platinum, making a voltaic couple by immersing them in dilute common salt solution. The circuit is kept complete for 24 hours, and the potential of the two electrodes by this process is nearly equalised. Perfect equality is secured by repeated warming and cooling of the solution and by sending through the circuit an alternating current which is gradually reduced to zero. I have by this means been able to obtain two electrodes which are iso-electric. The specially prepared electrodes (made of gold or platinum wire) are put in connection with the plant through kaolin paste moistened with normal saline solution. Care should be taken to put an opaque cover over the plant-holder, so as to guard against any possible photo-electric action; moistened blotting-paper maintains the closed chamber (not shown in fig. 190) in a uniform humid condition.

THREE DIFFERENT METHODS OF OBSERVATION

For serving definite experimental purposes I have employed three different methods: (1) The Method of Contact with Sensitive and Indifferent Points; (2) the Method of Axial Rotation; and (3) that of Vertical Rotation.

Method of contact with sensitive and indifferent points.—This is the most perfect method, for in it the indifferent distant point is unaffected by geotropic action. An example will make the matter clear. In the Water-Lily (*Nymphaea*) it is the peduncle which is sensitive to geotropic stimulus. One electric contact is made at an indifferent point on a sepal, which is always kept vertical; the other is made at a point A on one side of the peduncle (fig. 193).

Experiment 175. *Induced electric variation on upper side of the organ.*—The sepal being held vertical, the peduncle

is horizontal, so that the point A is above. Geotropic stimulation is at once followed by a responsive current which flows through the galvanometer from N to A, the upper side of the organ then exhibiting excitatory reaction of galvanometric negativity (right-hand illustration, fig. 193). When the peduncle is brought back to the vertical position, geotropic stimulation disappears, and with it the responsive current.

Experiment 176. *Electric variation on the lower side.*—The peduncle is now displaced through $-90°$, so that the

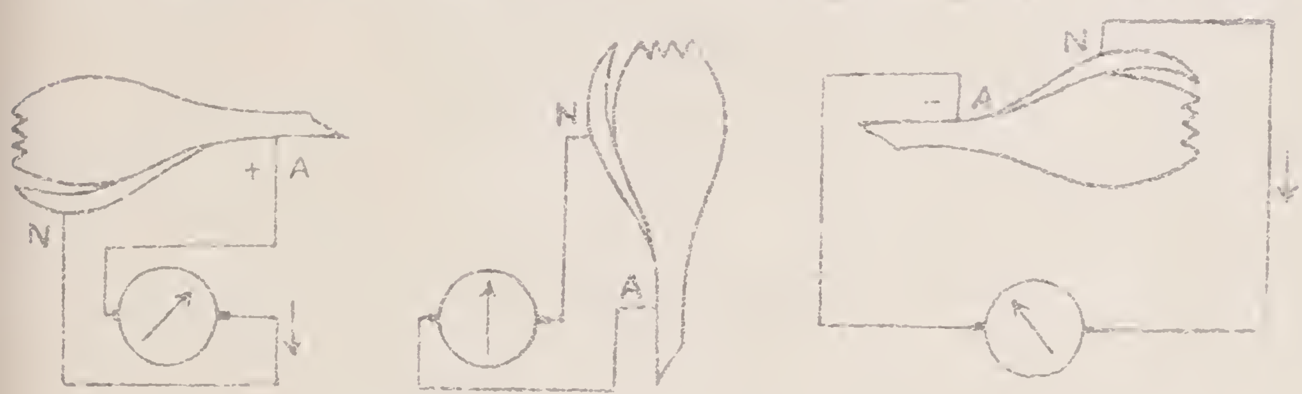


FIG. 193. Diagrammatic representation of geo-electric response.

The middle figure represents vertical position. In figure to the right, rotation through $+90°$ has placed A above with induced electric change of galvanometric negativity at A. In the figure to the left, rotation is through $-90°$, A being below. The electric response is induced galvanometric positivity at A. For simplification of the diagram, the vertical position of the scapes is not always shown.

point A, which under rotation through $+90°$ faced upwards, is now made to face downwards. The direction of the current of response is now found to have undergone a reversal; it now flows from A on the lower side to the indifferent point N; thus under geotropic action the lower side of the organ exhibits galvanometric positivity (left-hand illustration, fig. 193).

It is obvious that when electric connections are made on two diametrically opposite sides A and B of the shoot, inclination of the organ through 90° to the vertical makes the upper side A galvanometrically negative whilst the lower side B is rendered galvanometrically positive. The resulting electromotive variation is therefore additive. Such

connections are made in the two methods of Axial and Vertical Rotation.

Method of Axial Rotation.—The principle of this method has already been explained (*cf.* fig. 190). It is diagrammatically represented in fig. 194, H.

Method of Vertical Rotation is diagrammatically represented in fig. 194, V. The specimen is held vertical and electric contacts, A and B, made on two opposite sides; it is then rotated round a horizontal axis perpendicular to the long axis of the specimen. For the purpose of simplicity

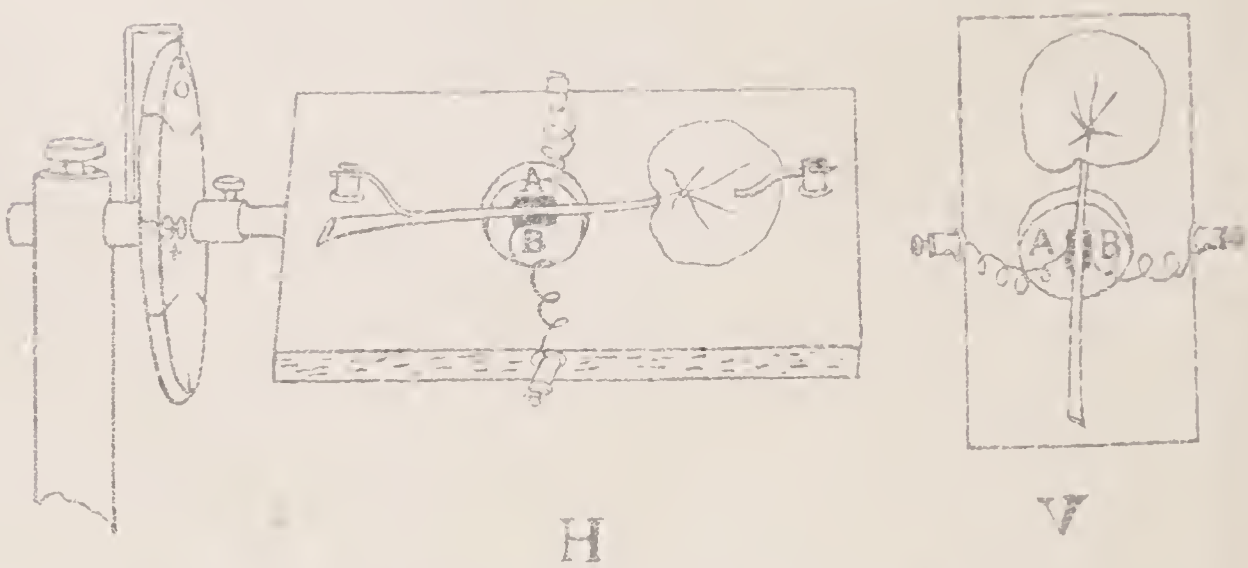


FIG. 194. Diagrammatic representation of the Method of Axial Rotation H, and of Vertical Rotation V (*see* text).

I confine attention to the electric change induced at the upper side of the organ. Rotation may be begun in a right-handed direction, making an increasing angle with the vertical, when the point A is subjected to increasing geotropic stimulation and exhibits increasing electric change of galvanometric negativity. Continuous decrease of the angle of inclination to zero by rotation in the reverse direction causes a disappearance of the induced electric change. The rotation is next continued in the left-handed direction, by which the point B is subjected to increasing geotropic stimulation. B is now found to exhibit excitatory reaction, the current of response having undergone a reversal. Rotation to the right and left may be distinguished by plus and minus signs.

Characteristics of Geo-Electric Response

There are certain phenomena connected with the electric response under geotropic stimulation which appear to be highly significant. According to the statolithic theory:

'Geotropic response begins as soon as an organ is deflected from its stable position, so that a few starch-grains press upon the ectoplasts occupying the walls which are underneath in the new position; an actual rearrangement of the starch-grains is therefore not an essential condition of stimulation. As a matter of fact, the starch-grains do very soon migrate on to the physically lower walls, when a positively or negatively geotropic organ is placed horizontally, with the result that the intensity of stimulation gradually increases, attaining its maximum value when all the falling starch-grains have moved on to the lower region of the ectoplast. The time required for the complete rearrangement of the statoliths may be termed the period of migration; its average length varies from five to twenty minutes in different organs.' [1]

Stimulation, according to the statolithic theory, is induced by the displacement of solid particles. The diameter of the geotropically sensitive cells is considerably less than 0·1 mm.; and the stimulus will be perceived after the very short interval taken by the statoliths to fall through a space shorter than 0·1 mm. This may be somewhat delayed by the viscous nature of the plasma, but in any case the period for perceptible displacement of the statoliths should be very short, about a few seconds, and the latent period of perception of stimulation should be of this order.

The mechanical indication of response to stimulus is delayed by a period which is somewhat indefinite; for the initiation of responsive growth-variation will necessarily lag behind the incidence of stimulus.

Experiment 177.—The mechanical response is thus

[1] Haberlandt, *Physiological Plant Anatomy* (1914), p. [illegible].

incapable of giving an accurate value of the latent period. The electric method of investigation labours under no such disadvantage: for, since the excitation is hereby detected independently of movement, the incidence of stimulus is followed by response without any undue delay. I will give a record of the electric response of the quickly reacting

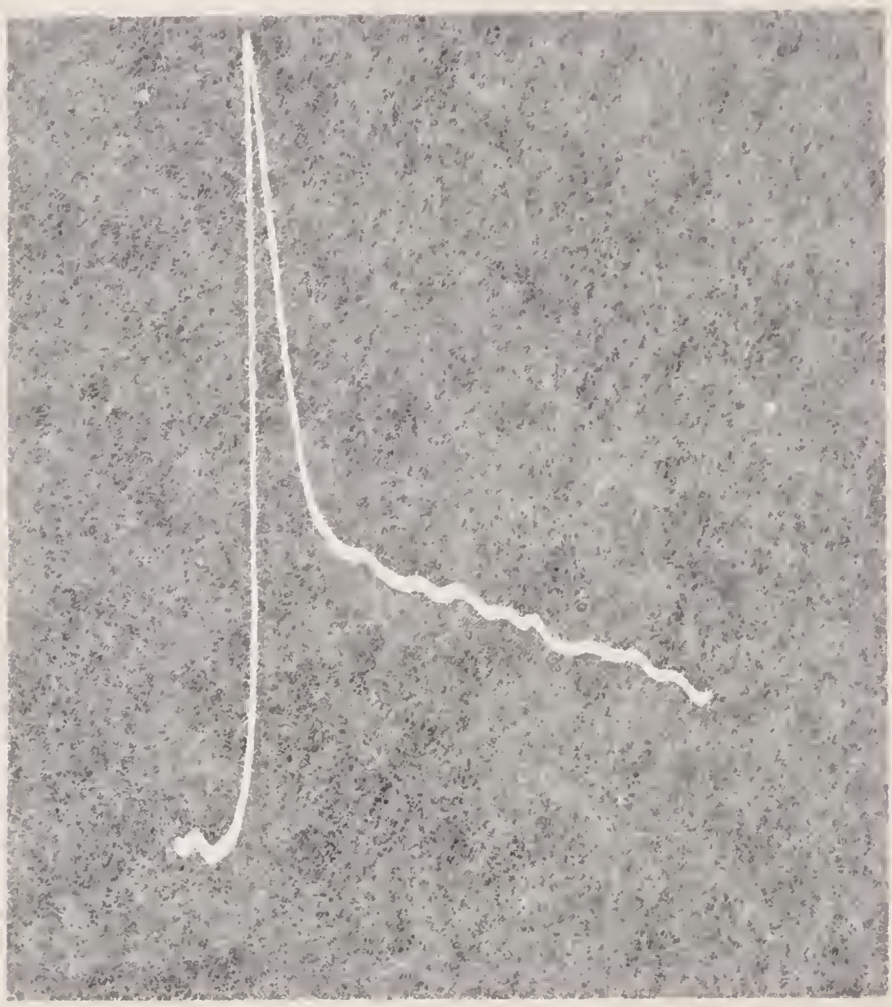


FIG. 195. Geo-electric response of Anthurium. Latent period shorter than 5 seconds.

peduncle of Anthurium, when the angle of inclination was increased from zero to 90°. The responsive movement of the galvanometer spot of light was initiated in less than 5 seconds and the maximum deflection was reached in the course of about 30 seconds. The angle was next reduced to zero, and the deflection practically disappeared in the further course of a minute and a half (fig. 195). There was a small 'excitation remainder': but with vigorous specimens the recovery is completed in a short time.

The latent period of the mechanical response of the

petiole of Tropaeolum is also a few seconds, a value which is quite consonant with the idea of particles inducing excitation by their fall through an exceedingly short distance. In less sensitive organs the latent period is protracted for reasons that have already been given (p. 284).

PHYSIOLOGICAL CHARACTER OF GEO-ELECTRIC RESPONSE

The intensity of the electromotive variation is found to depend on the physiological vigour of the specimen. The Tropaeolum plants often employed in my experiments are in the best condition of growth in Calcutta in February; after this the plants begin to decline in March and die off by the end of April.

Experiment 178.—In February the intensity of electric response was nearly double of that in March; it was only in March that I could construct an accurate potentiometer for quantitative determination of the induced electromotive force between the upper and lower contacts on rotation of the specimen from zero to 90°. I give below the following typical values obtained with two different specimens:

Specimen	Induced E.M.F.
(1)	12 millivolts
(2)	15 ,,

Effect of Age.—While a young petiole gave the above value, an old specimen from the same plant exhibited no response. The plants were in a dying condition in April and all indications of electric reaction were found to be abolished.

RELATION BETWEEN ANGLE OF INCLINATION AND GEOTROPIC EXCITATION

In the Method of Axial Rotation, experimental conditions are ideally perfect. In the neutral position the sides A and B are both parallel to the vertical lines of gravity, and are little affected by geotropic reaction. At

the specimen is rotated on its long axis, the vertical component of the force of gravity increases with the angle of inclination. The hypothetical statolithic particles will become displaced all along the cells, and the vertical pressure exerted by them will also increase with the angle.

Experiment 179.—The specimen was rotated through 45° and the maximum electric response observed. The angle was next increased to 90° and the reading for the enhanced response taken. The ratio of the geo-electric response at 90° and 45° thus affords a measure of the effective stimulation at the two angles. I give below a table of the results obtained with twenty-four different specimens.

TABLE XX.—RELATION BETWEEN ANGLE OF INCLINATION AND GEOTROPIC EXCITATION.

No. of specimen	Galvanometric deflection		Ratio $\frac{b}{a}$
	(*a*) at 45°	(*b*) at 90°	
1	70 divisions	110 divisions	1·5
2	30 ,,	45 ,,	1·5
3	90 ,,	126 ,,	1·4
4	70 ,,	100 ,,	1·4
5	21 ,,	33 ,,	1·6
6	30 ,,	50 ,,	1·6
7	12 ,,	20 ,,	1·6
8	14 ,,	20 ,,	1·4
9	10 ,,	16 ,,	1·6
10	45 ,,	75 ,,	1·5
11	25 ,,	40 ,,	1·6
12	14 ,,	20 ,,	1·4
13	13 ,,	20 ,,	1·5
14	30 ,,	50 ,,	1·5
15	38 ,,	54 ,,	1·4
16	50 ,,	75 ,,	1·5
17	55 ,,	90 ,,	1·5
18	13 ,,	20 ,,	1·5
19	17 ,,	25 ,,	1·4
20	80 ,,	130 ,,	1·5
21	15 ,,	22 ,,	1·4
22	45 ,,	75 ,,	1·5
23	135 ,,	220 ,,	1·6
24	55 ,,	85 ,,	1·5
Mean ratio = 1·49			

The mean ratio 1·49 may thus be regarded as that of the geotropic reactions at 90° and 45°; this is practically the same as $\frac{\sin 90^\circ}{\sin 45^\circ} = 1 \cdot 4$, which may be stated as the following law:

The intensity of geotropic reaction varies as the sine of the directive angle.

The results obtained with the Method of Vertical Rotation will be described in a subsequent chapter.

Summary

The excitatory response to geotropic stimulation has been discovered by the electrical method, the sign of excitation being an electromotive change of galvanometric negativity.

In addition to the method of contact with an indifferent point, two other methods have been rendered practical, the methods of Axial and of Vertical Rotation. The upper side of a horizontally laid shoot is found to undergo an excitatory change of galvanometric negativity.

In quickly reacting organs the latent period of geo-electric response is about 5 seconds, and the maximum excitation is induced in the course of less than 2 minutes.

Under symmetrical conditions the intensity of geotropic reaction is found to be proportional to the sine of the angle of inclination.

CHAPTER XXX

LOCALISATION OF GEO-PERCEPTIVE LAYER BY ELECTRIC PROBE

Having found that plant-organs are sensitive to geotropic stimulation, the question arises as to the distribution of the cells which perceive the stimulus, the impulse from which causes neighbouring cells to carry out a movement of orientation in a definite direction. Are the perceptive cells diffusely distributed in the plant or do they form a definite layer? Would it be at all possible to localise the sensitive cells in the interior of the organ?

It is true that post-mortem examination of sectioned tissues under the microscope suggested the statolith theory, according to which the contents of certain cells cause geotropic excitation. But for the clear understanding of the physiological reaction which induces the orientating movement, it is necessary to get hold, as it were, of the sensory cells in a condition of full vital activity; to detect and follow the changes induced in the perceptive organ and the irradiation of excitation to neighbouring cells, through the entire cycle of reaction from the onset of geotropic stimulation to its cessation.

The idea of obtaining access to the hypothetical geo-perceptive cells in the interior of the organ would appear at first sight to be almost hopeless; the problem has been, however, solved by the invention of the Electric Probe, by which it has been possible to locate the excitatory electric conditions in the interior of the plant.

The principle of the method will be readily understood from the following. As every side of a radial organ is geotropically excitable, the geo-perceptive cells must be disposed in a cylindrical layer at some unknown depth from the surface, which, in a longitudinal section of the shoot, would appear as two straight lines G and G′ (fig. 196). In a vertical position the geo-perceptive layer will be electrically neutral, but rotation through 90° will initiate an excitatory

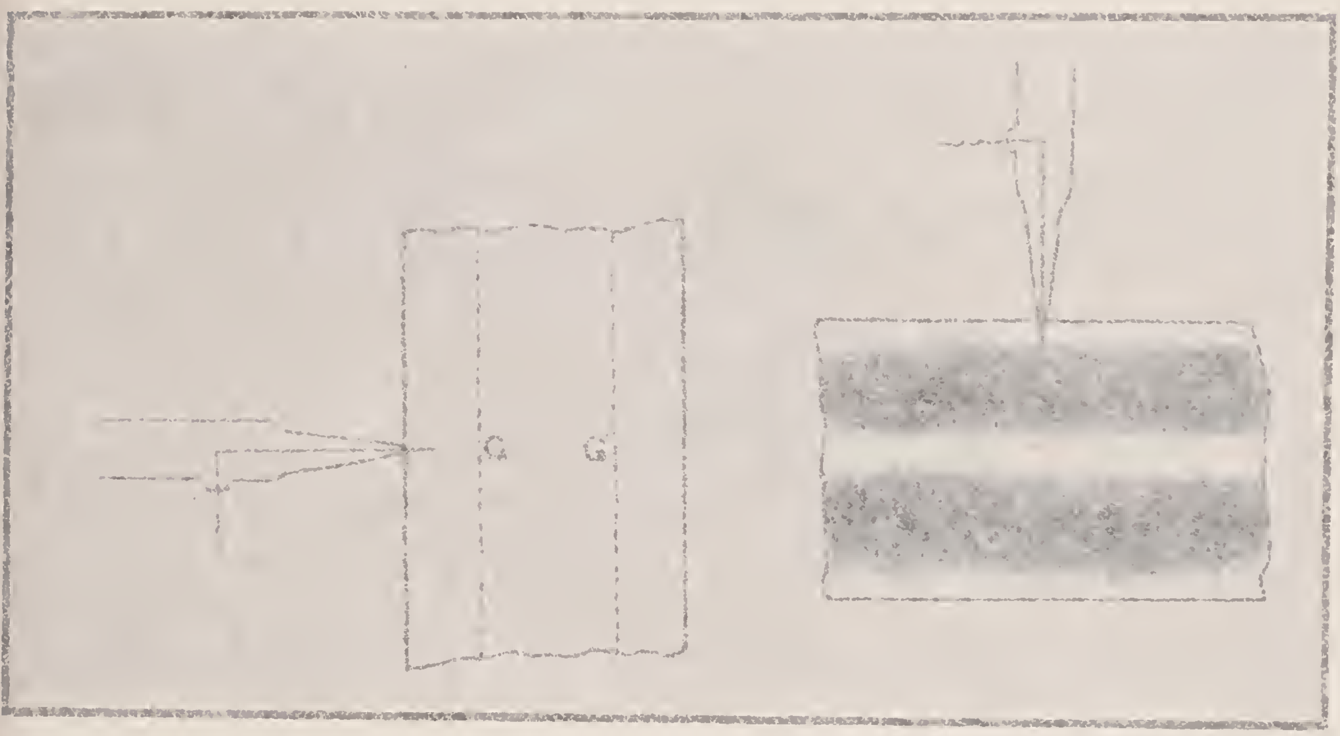


FIG. 196. Diagrammatic representation of the geo-perceptive layer in unexcited vertical and in excited horizontal position (see text)

reaction. This sensitive tissue will then respond to the stimulus and become the focus of excitation, the state of excitation being detectable by accompanying galvanometric negativity, which would be most intense at the perceptive layer itself. The excitation of the perceptive layer will irradiate into the neighbouring cells in radial directions with diminishing intensity, reaching the cortical cells which effect the curvature.

The distribution of the excitatory change, initiated at the perceptive layer and irradiated in radial directions, is represented by the depth of the shading, the darkest shadow being on the perceptive layer itself (fig. 196). Were

excitation attended with a change from light to shade, there would be witnessed the spectacle of a deep shadow (vanishing towards the edges) spreading over the different layers of cells during displacement of the organ from the vertical to the horizontal; the shadow would disappear on the restoration of the organ to the vertical position.

THE ELECTRIC PROBE

Different intensities of excitation in different layers are capable of detection by means of the Electric Probe, insulated except at the tip, which is gradually forced into a horizontal stem from the surface (fig. 197). Increasing

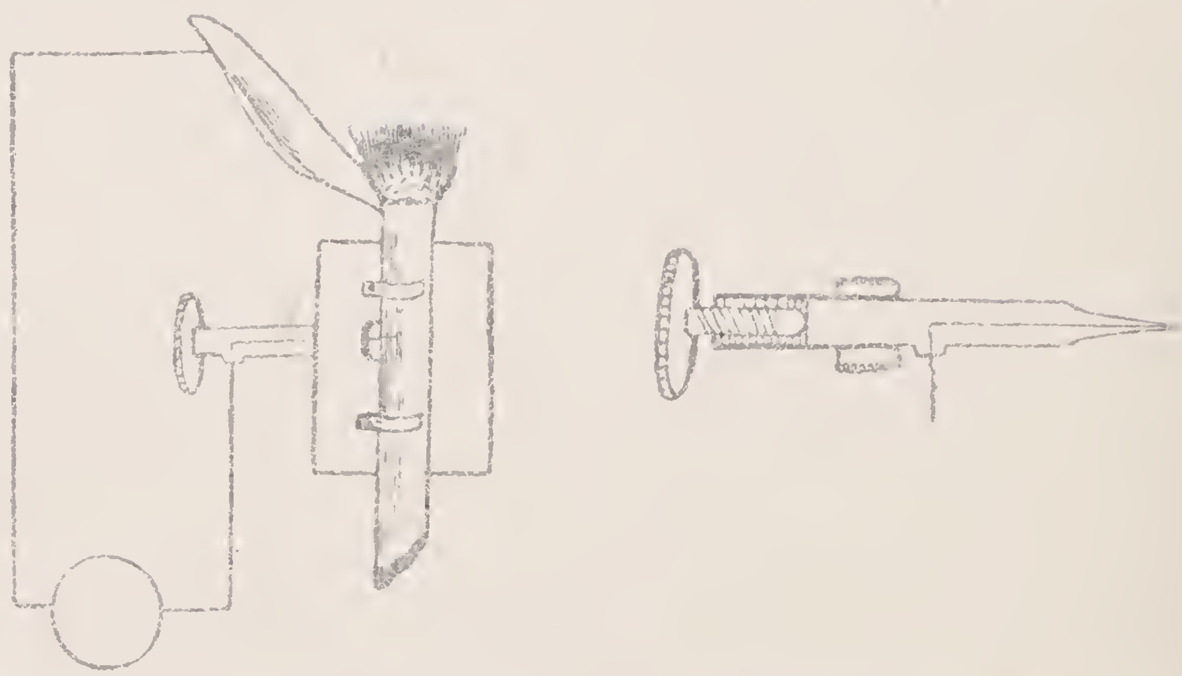


FIG. 197. The Electric Probe.

Figure to the left represents one electric contact made with a sepal of Nymphaea, and the other with the peduncle by means of the Probe; the included galvanometer is represented by a circle. Figure to the right is an enlarged view of the Probe.

excitatory change of galvanometric negativity will be exhibited as the probe approaches the perceptive layer at which the electric excitation will be maximum. After this, as the probe passes beyond the perceptive layer, the electric indication of excitation undergoes decline and final abolition. The characteristic excitation occurs only under

the action of gravitational stimulus: it will disappear when the organ is held in a vertical position and thus freed from geotropic excitation.

ACTUAL OBSERVATIONS

The degree of the induced galvanometric negativity of the upper side of the horizontal stem was found to exhibit variation at different depths, and to attain a maximum value at a definite layer, beyond which there is a decline. The geo-perceptive layer can thus be experimentally localised by measuring the depth of the intrusion of the probe at which the maximum galvanometric negativity is detected.

The electric response of the lower side of the organ to gravitational stimulus is of an opposite sign to that of the upper side, galvanometric positivity, indicative of expansion and increase of turgor. The electric indications on the lower side also exhibit variation in the different layers, the maximum positivity occurring at the perceptive layer.

In animals it has been found that the weight of heavy particles acting on sensitive protoplasm causes the perception of the direction of gravity. From histological considerations Haberlandt and Němec came to the conclusion that heavy particles, such as starch-grains, perform a similar function in many plants. The electro-physiological investigation which I undertook had as its objects the exact localisation of the sensory cells in a living condition, and, as already stated, the recording of the changes accompanying their functional activity under geotropic stimulation. The electric results obtained fully confirm the statolith-theory in the conclusion that it is the 'starch-sheath,' containing a number of large-sized starch-grains, which is the geo-perceptive organ.

THE METHOD OF EXPERIMENT

In the practical application of the probe the difficulty anticipated was the after-effect of the wound inducing

variation of excitability in the different layers of tissue. The wound-irritation is, however, reduced to a minimum by making the probe exceedingly thin. A fine platinum wire, 0·06 mm. in diameter, passes through a glass tube drawn out into a fine capillary and fused round one end of the platinum wire, which protrudes very slightly beyond the point of fusion; the exploring electrode is thus insulated except at its protruding sharp point. The length of the capillary is, generally speaking, about 6 mm., just long enough to traverse the experimental plant-organ transversely from one side to the other; the average diameter of the capillary is about 0·15 mm. The other end of the platinum wire comes out of the end of the glass tube and is led to one terminal of the galvanometer, the other being connected with an indifferent point on the organ. The probe can be gradually forced into the plant-organ by rotation of a screw-head, one complete rotation causing a forward movement through 0·2 mm.

Prick-reaction.—A prick acts as a mechanical stimulus, and in normal excitable tissues induces an excitatory change of galvanometric negativity; this prick-reaction increases with the extent of the wound, and the suddenness with which it is inflicted. On account of the fineness of the probe, it insinuates itself into the tissue without making any marked rupture; the probe is, moreover, introduced very gradually; with these precautions the reaction due to prick is found to be greatly reduced. The immediate effect of the prick is a negative deflection of the galvanometer, which declines and attains a steady value in the course of a few minutes. The depressing effect of the passage of the probe on geotropic excitability disappears, I find, in the course of about 10 minutes.

In the choice of experimental material it is necessary to find specimens which are not merely geotropically sensitive, but also give a large electric response under stimulation. In these respects the petiole of Tropaeolum, the peduncle of Nymphaea, and the shoot of Bryophyllum,

in their proper seasons, give good results. For the success of the following experiments, it is essential that the plant should be in an exceptionally vigorous condition.

Distribution of Excitability in the Petiole of Tropaeolum

Detailed results of the experiments on the localisation of the geo-perceptive layer in the petiole of Tropaeolum are given below as typical. The petiole of Tropaeolum has the following special advantages. Geotropically it is very sensitive; its latent period of response is very short, the horizontally laid petiole beginning to bend upwards in the course of a short time. The leaf may be isolated from the plant, and the cut end of the petiole placed in moist cotton. The normal geotropic irritability of the cut specimen is found to be fully restored in the course of half an hour. The manipulation of a cut specimen, placed alternately in a vertical and in a horizontal position, presents no difficulty. A very large number of specimens can be, moreover, obtained from the same plant. As regards geotropic reaction, the induced electromotive variation of the petiole of Tropaeolum is considerable and attains the maximum value within a few minutes; the recovery is practically complete after restoration to the vertical.

The mode of experimental procedure (slightly different from what has already been described) is as follows: the probe is thrust into the petiole by successive steps of 0·05 mm., and the electric response observed on displacement of the petiole from the vertical to the horizontal position, in which latter position the organ is subjected to geotropic stimulation. The induced electric variation, as already stated, is of considerable intensity. The irritation caused by the prick of the probe is very slight, the immediate effect of the insertion of the probe being a negative deflection

of the galvanometer which declines and practically disappears in the course of about 5 minutes. The geotropic irritability is fully restored in the course of about 10 minutes, after which a record of the geotropic response may be taken.

Experiment 180. *Geo-electric response at different depths.*—I give below the photographic records of the

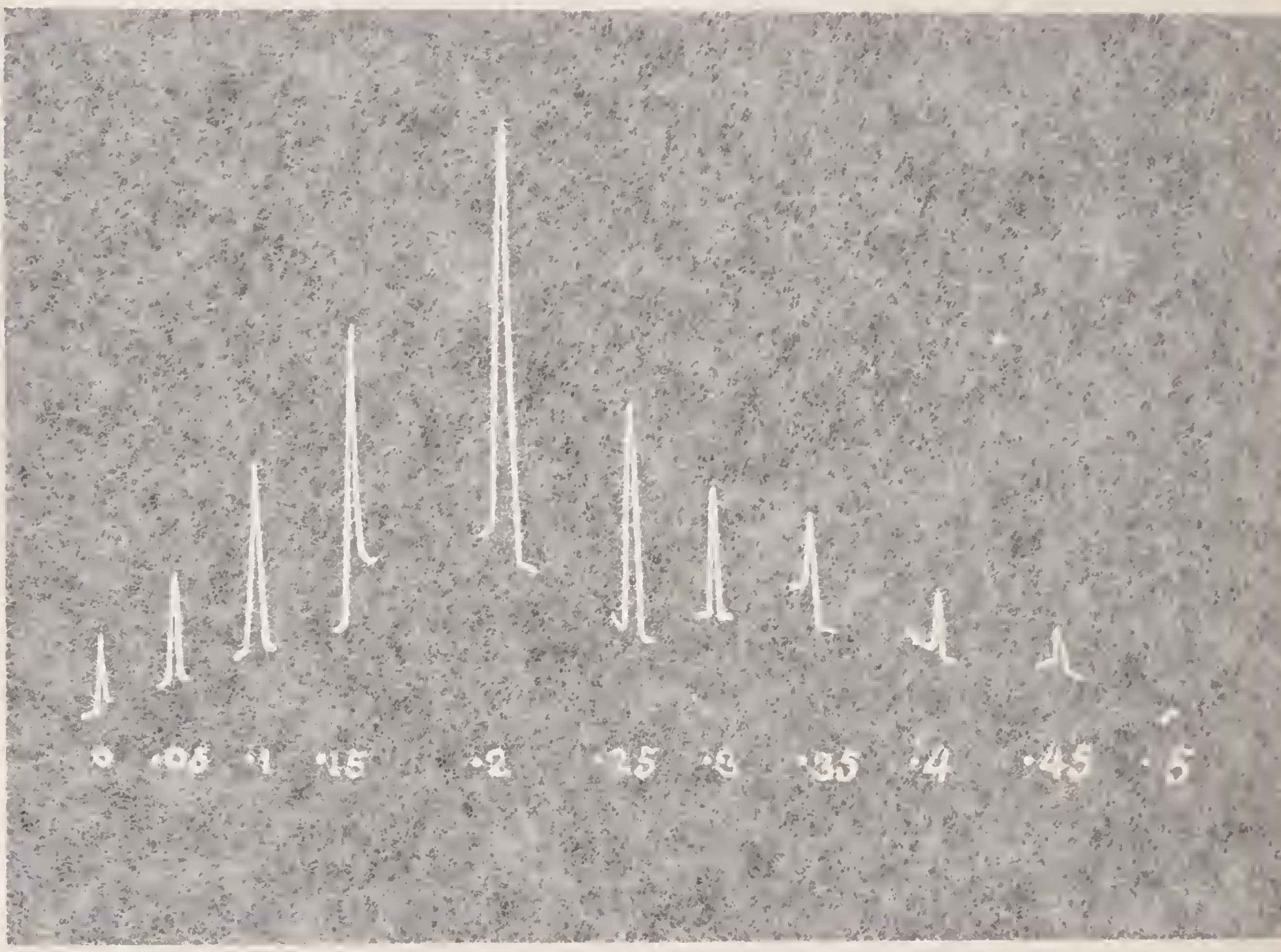


FIG. 198. Intensity of geo-electric response at different depths in the petiole of Tropaeolum.

Note the maximum excitation at a depth of 0·20 mm.

response to the stimulus of gravity at different depths as the probe was thrust in from outside by successive steps of 0·05 mm. (fig. 198). It will be seen that the geo-electric response underwent a continuous increase till the maximum excitation occurred at a depth of 0·20 mm. A rapid decline occurred beyond this point, and the response disappeared at a depth of 0·50 mm. The following table gives the quantitative results of the experiment:

TABLE XXI.—SHOWING GEO-ELECTRIC RESPONSE AT DIFFERENT DEPTHS IN THE PETIOLE OF TROPAEOLUM.

Distance from surface in mm.	Geo-electric response of galvanometric negativity
0·00	5 divisions
0·05	9 ,,
0·10	18 ,,
0·15	29 ,,
0·20	**42** ,,
0·25	20 ,,
0·30	11 ,,
0·35	7 ,,
0·40	5 ,,
0·45	2 ,,
0·50	0 ,,

Position of the starch-sheath was at a depth of 0·20 mm.

Subsequent microscopic examination showed that the maximally excited layer at the depth of 0·20 mm. was that which contains the starch-grains. The geo-perceptive layer is thus found to coincide with the starch-sheath.

Maximum excitability at the geo-perceptive layer.—The maximum excitation induced at the perceptive layer appears to be due to two factors: first, the direct stimulation caused by the fall of the starch-grains; secondly, the greater *general excitability* of the geo-perceptive layer as compared with that of the neighbouring ones. The relatively greater excitability of the perceptive layer became evident from the effects observed during the passage of the probe with the specimen held vertical, when there was no geotropic stimulation. The insertion of the probe then acts as a mechanical stimulus, and the response of galvanometric negativity is found to be maximum at or near the starch-sheath, proving that this is relatively the most excitable. The response to prick takes place *during* the thrust of the probe; the resulting irritation disappears, however, when the probe is left stationary. The normal excitability of the cells is restored, as already stated, after a period of rest of about 10 minutes.

The following table gives the results obtained with twelve different specimens of the petiole of Tropæolum. The specimens were unequally thick; hence the sensitive layer was found at a depth of 0·15 mm. in thin and at 0·20 mm. in thick, specimens; the maximum electric excitation was in all cases found to occur at the starch-sheath.

TABLE XXII.—GEO-ELECTRIC REACTION AT VARIOUS DEPTHS IN DIFFERENT SPECIMENS (PETIOLE OF TROPÆOLUM).

No. of Specimen	Responsive galvanometric negativity at depth of							Position of starch-sheath below surface
	0 mm.	0·1 mm.	0·15 mm.	0·2 mm.	0·25 mm.	0·3 mm.	0·4 mm.	
	Divs.	Divs.	Divs.	Divs.	Divs.	Divs.	Divs.	Mm.
1	7	10	50	35	15	0	0	0·16
2	10	21	47	84	95	57	7	0·20
3	0	6	10	25	8	2	0	0·20
4	5	35	57	30	19	13	0	0·15
5	0	15	22	30	21	15	0	0·10
6	5	8	15	[illegible]	4	1	0	0·15
7	3	5	14	[illegible]	3	0	0	0·15
8	0	16	31	46	14	12	8	0·20
9	3	12	15	11	8	0	0	0·15
10	2	10	22	7	3	[illegible]	0	0·15
11	3	18	52	45	35	20	7	0·21
12	0	–	5	20	7	3	0	0·2[illegible]

DECLINE OF GEOTROPIC EXCITABILITY AT DISTANCE FROM THE PERCEPTIVE LAYER

The experimental localisation of the perceptive layer is greatly facilitated by the abrupt enhancement of excitation at that layer. This will be fully realised from the resultant curve obtained from data derived from twelve different specimens. Taking the perceptive layer itself as the point of reference, successive distances, say, of 0·05 mm. are measured to the left and to the right of the point of reference. The abscissa to the left is towards the centre of the petiole, that to the right towards the surface. The mean values of the excitatory reactions at the different points are the ordinates for the curve. It

will be seen how abruptly it rises to the maximum at the perceptive layer and falls beyond it inwards and outwards (fig. 199).

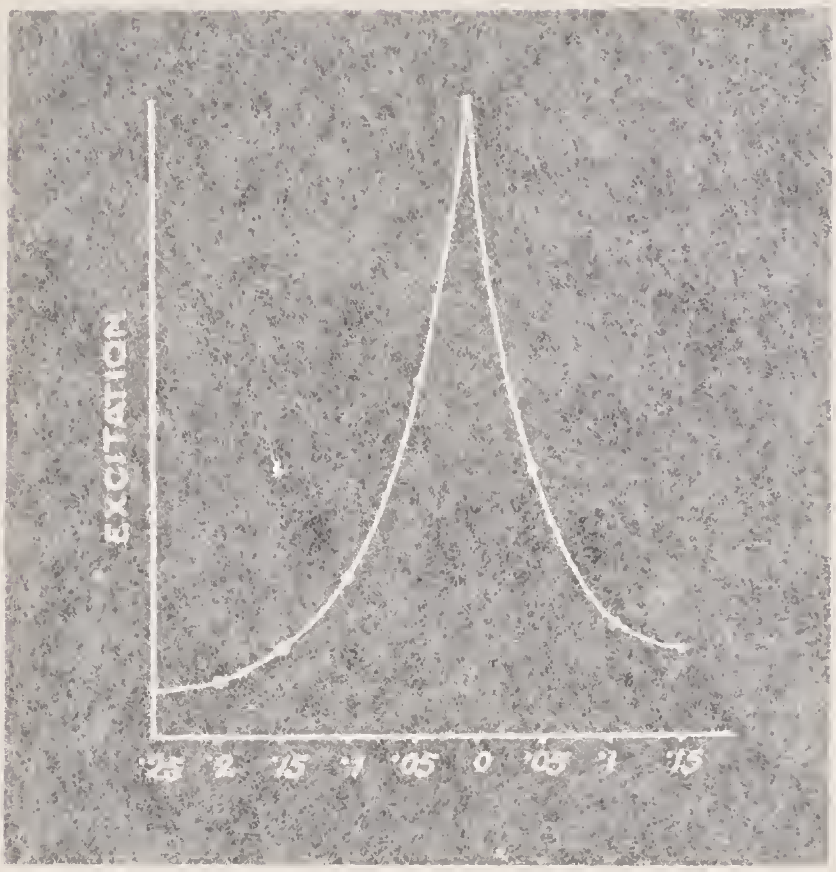


FIG. 199. Curve showing distribution of geotropic excitability. Maximum excitation occurs at geo-perceptive layer 0. Excitatory reaction rapidly declined inwards and outwards.

The geo-perceptive layer may thus be experimentally localised by measuring the depth of intrusion of the probe at which maximum deflection of galvanometric negativity is found to occur.

Opposite Reactions in Upper and Lower Halves

The experiments with Tropaeolum, Nymphaea, and Bryophyllum brought out the striking fact that under the stimulus of gravity the excitatory electric reaction in the lower half is of opposite sign to that in the upper half, a positive instead of a negative electric variation, the maximum positivity occurring at the lower starch-sheath. Since galvanometric negativity is associated with contraction

and galvanometric positivity with expansion, the geotropic curvature of the stem or the petiole is thus due to the joint effect of contraction in the upper and expansion in the lower half. Some difficulty may be encountered in finding a satisfactory explanation of the two opposite reactions, but the following considerations will help to remove it. The facts established are:

1. That the upper half of the horizontal shoot undergoes contraction under geotropic stimulation
2. That the lower half undergoes expansion.
3. That the pressure on the protoplasm in the cells of the starch-sheath, exerted by the heavy particles, is the cause of stimulation.
4. That the particles press on the inner tangential ectoplasmic layer of the sensitive cells in the upper, and on the outer tangential ectoplasmic layer in the lower, half. A reasonable explanation of the opposite reactions of the upper and lower halves may probably be found in the unequal excitability of the protoplasmic layer on different sides of the sensitive cell. It will be shown (p. 356) that the excitability of the ectoplasmic layer at the apical end of the geo-perceptive cells is greater than at the basal end. It will therefore be natural to expect that a similar difference of excitability exists between the ectoplasmic layers lining the inner and the outer tangential walls of the cells (*see* fig. 180), so that pressure of particles will induce maximal stimulation in the former and subminimal stimulation in the latter.
5. That while maximal stimulation induces retardation of growth culminating in actual contraction, subminimal stimulation causes expansion and enhancement of the rate of growth (p. 83).

Hence the opposite electric responses given by the upper and the lower sides of the organ can be explained on the not

unjustifiable assumption that in the first case the stimulation is maximal, while in the latter it is subminimal.

The following facts are of confirmatory value. In my 'Nervous Mechanism of Plants' it has been shown that the

FIG. 200.

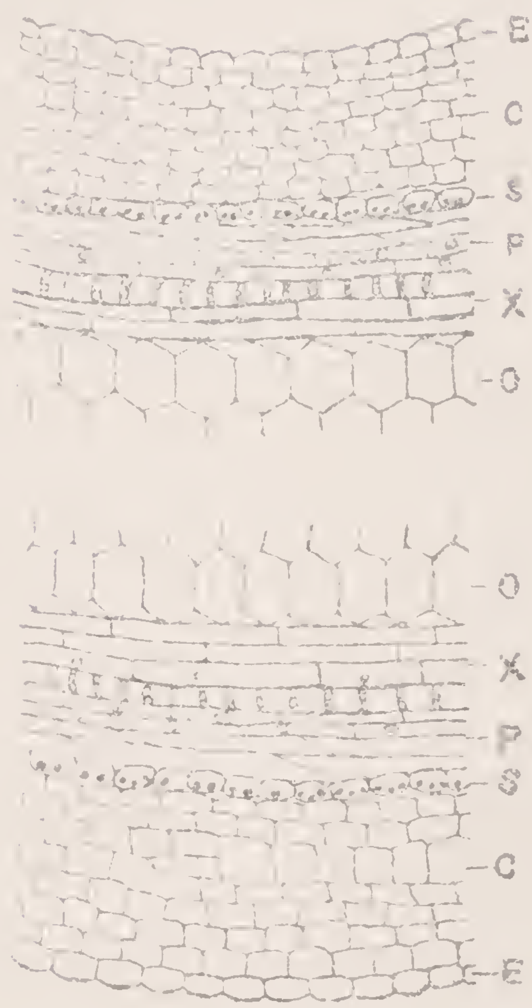


FIG. 201.

FIG. 200. Photo-micrograph of transverse section of upper half of horizontally laid stem of Impatiens.

Note the starch-grains fallen on to the inner tangential wall of statocysts S which abut on the phloem P.

FIG. 201. Longitudinal section of upper and lower halves of geotropically curved stem of Eclipta.

Note contraction of the upper and expansion of the lower cortex C. The starch-grains have fallen on the inner tangential wall of the upper statocysts (abutting on the phloem P). The starch-grains in the lower statocysts are lying against the outer tangential wall

phloem functions as a nervous tissue, and it may be of significance that the statocysts are situated in closest contiguity with the phloem.

Fig. 200 shows the transverse section of the upper half

of the stem of Impatiens made shortly after it had been placed in a horizontal position. The starch-grains are seen to have fallen on to the inner tangential wall of the statocysts which abut on the phloem. Geotropic curvature has been explained to be due to the joint effect of contraction of the upper and expansion of the lower side. What is the difference in the stimulating mechanism of the geo-perceptive cells of the upper and lower halves? Taking a seedling of Eclipta which is highly sensitive to geotropic stimulation, it is laid horizontally, and a vertical longitudinal section made *after* the production of upward curvature. The illustration (fig. 201) shows the physiological changes induced in the two halves. The cortex in the upper half shows a relative *contraction*, while that in the lower half a relative *expansion*. The starch-grains in the upper statocysts are seen to press against the *inner tangential wall* of the cells nearest the phloem; in the lower half of the stem, the starch-grains in the cells are, on the other hand, pressing on the *outer tangential wall* furthest from the phloem. It is important to bear in mind this characteristic difference in the stimulation of the two halves of the organ.

Method of Transverse Perforation

Experiment 181.—I next carried out a complete exploration of the interior of the peduncle of Nymphaea along its diameter. The probe started from the upper surface and came out at the lower by successive steps of 0·2 mm., the corresponding geo-electric response being observed at each step. The successive readings were taken after right-handed rotation from the vertical to 90°; the rotation was never carried out in the left-handed direction to −90°. The probe, entering from above, passed through a region giving negative electric variation; and then beyond the central axis entered a region where the galvanometric indication was positive.

TABLE XXIII.—SHOWING THE DISTRIBUTION OF GEOTROPIC EXCITABILITY THROUGH THE PEDUNCLE OF NYMPHÆA (DIAMETER = 6·8 MM.)

Position of probe	Galvanometer deflection	Position of probe	Galvanometer deflection
Surface	— 10 divisions	3·6 mm.	0 divisions
0·2 mm.	— 25 ,,	3·8 ,,	0 ,,
0·4 ,,	— 40 ,,	4·0 ,,	0 ,,
0·6 ,,	— 50 ,,	4·2 ,,	2 ,,
0·8 ,,	— 62 ,,	4·4 ,,	4 ,,
1·0 ,,	— 72 ,,	4·6 ,,	5 ,,
1·2 ,,	— 88 ,,	4·8 ,,	11 ,,
1·4 ,,	— 108 ,,	5·0 ,,	22 ,,
1·6 ,,	— 72 ,,	5·2 ,,	38 ,,
1·8 ,,	— 41 ,,	5·4 ,,	46 ,,
2·0 ,,	— 30 ,,	5·6 ,,	40 ,,
2·2 ,,	— 18 ,,	5·8 ,,	32 ,,
2·4 ,,	— 10 ,,	6·0 ,,	24 ,,
2·6 ,,	— 5 ,,	6·2 ,,	18 ,,
2·8 ,,	— 2 ,,	6·4 ,,	12 ,,
3·0 ,,	0 ,,	6·6 ,,	6 ,,
3·2 ,,	0 ,,	6·8 ,,	3 ,,
3·4 ,,	0 ,,	...	...

LOCALISATION OF GEO-PERCEPTIVE LAYER

A curve constructed from the data given above is seen in fig. 202. The diameter of the peduncle was 6·8 mm. The negative geo-electric response is seen to increase till it attains a climax at the depth of 1·4 mm. It then shows a continuous diminution till it becomes zero at the depth of 3 mm., where there is a neutral zone which extends through 1 mm. When the probe reaches a depth of 4·2 mm. measured from the upper side, it enters a region affected by the perceptive layer situated on the under side, the opposite physiological reaction being indicated by induced electric change of galvanometric positivity. This positivity reaches a climax at a depth of 5·4 mm. measured from the upper, and 1·4 mm. measured from the lower, surface. The points of maximum positivity and negativity are situated symmetrically in the two halves of the organ. The electric variation of maximum positivity in the lower half is

comparatively feeble, less than half the corresponding maximum negativity in the upper half. Microscopic section showed that the geo-perceptive layers were identical with the groups of statocysts forming the starch-crescents.

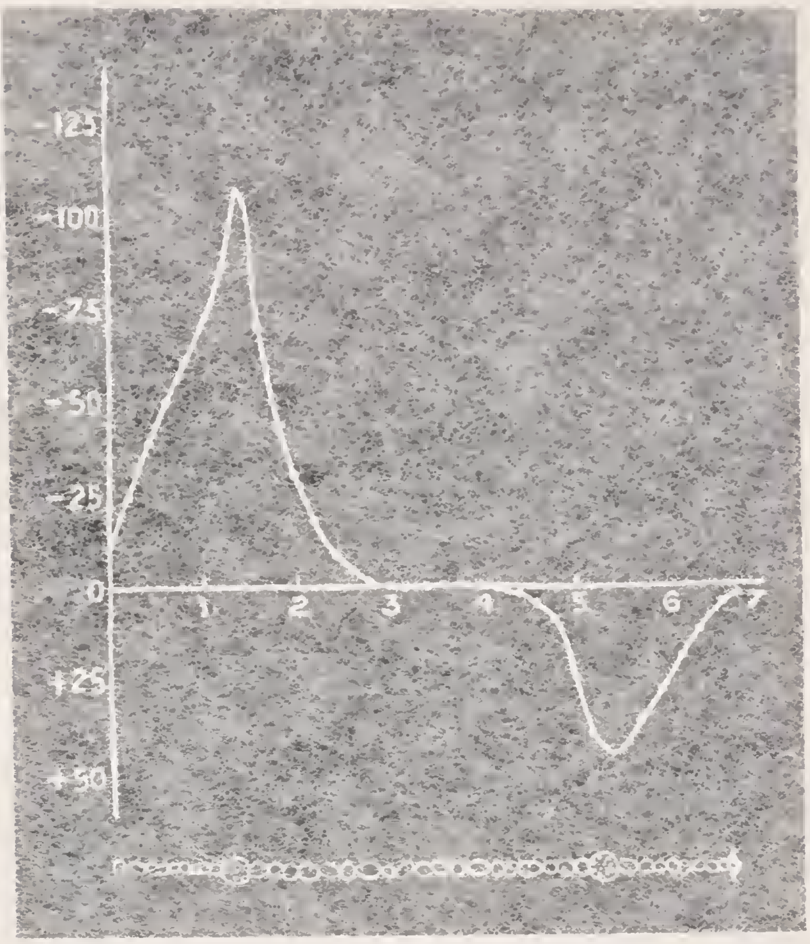


FIG. 202

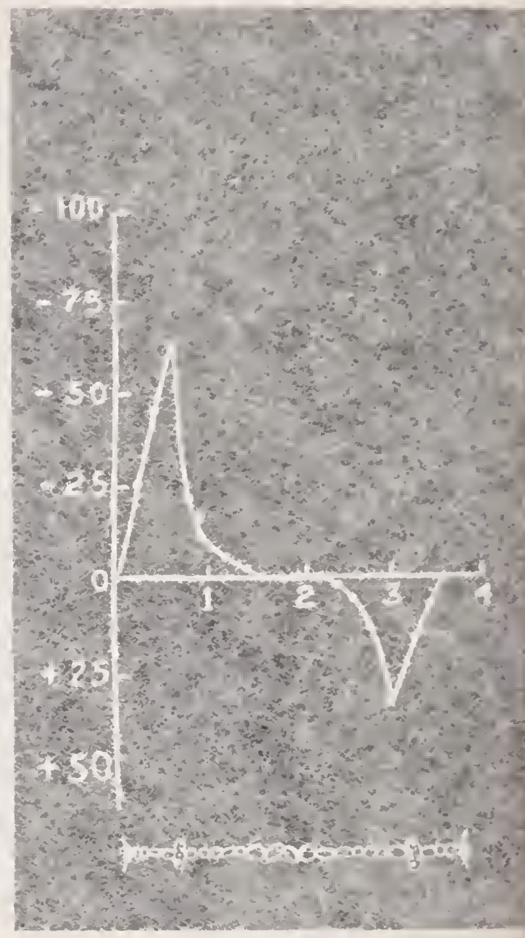


FIG. 203

FIG. 202. Distribution of geotropic excitability in the peduncle of Nymphaea. Ordinate represents geo-electric excitation; abscissa, distance from upper surface of flower-stalk. The diagrammatic section underneath shows the position of geo-perceptive layer (starch-sheath) corresponding to maximum induced galvanometric negativity and positivity in the two halves.

FIG. 203. Distribution of geotropic excitability in the shoot of Bryophyllum.

Experiment 182.—I carried out similar experiments with the shoot of Bryophyllum. The results are given in Table XXIV; the curve of the electric distribution along the diameter is given in fig. 203. The characteristics of this curve are the same as that of Nymphaea. The maximum galvanometric negativity occurred at the depth of

0·6 mm., and of positivity at a corresponding point on the opposite side.

TABLE XXIV.—SHOWING DISTRIBUTION OF GEOTROPIC EXCITABILITY THROUGH THE STEM OF BRYOPHYLLUM (DIAMETER = 3·6 MM.).

Position of probe	Galvanometric deflection	Position of probe	Galvanometric deflection
Surface	0 divisions	2·0 mm.	0 divisions
0·2 mm.	− 24 ,,	2·2 ,,	2 ,,
0·4 ,,	− 45 ,,	2·4 ,,	3 ,,
0·6 ,,	− **63** ,,	2·6 ,,	4 ,,
0·8 ,,	− 21 ,,	2·8 ,,	9 ,,
1·0 ,,	− 9 ,,	3·0 ,,	**36** ,,
1·2 ,,	− 6 ,,	3·2 ,,	21 ,,
1·4 ,,	− 3 ,,	3·4	9 ,,
1·6 ,,	0 ,,	3·6 ,,	0 ,,
1·8 ,,	0 ,,	...	...

After the electric test, transverse sections of the stem were made at the radial line of the passage of the probe. Thus, in a particular experiment with Bryophyllum, the point of maximum geo-electric response was found to be at a distance of 0·8 mm. from the surface. By means of the micrometer-slide on the stage of the microscope and the micrometer eye-piece, the layer 0·8 mm. from the surface was examined; this sensitive layer S was recognised as the *continuous* 'starch-sheath' or endodermis containing unusually large-sized starch-grains (fig. 204). These often occurred in loosely cohering groups of 8 to 10, and their appearance is very different from the small-sized irregularly distributed grains in other cells.

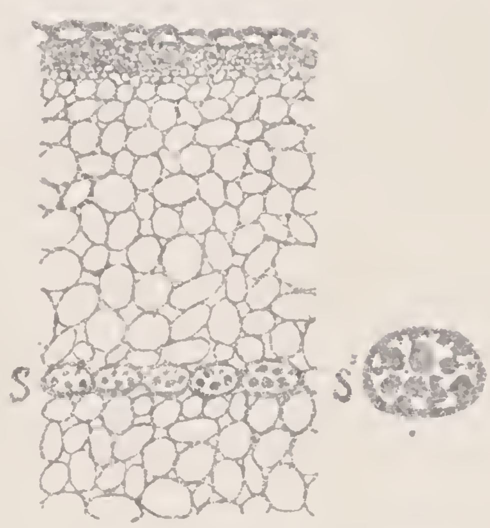


FIG. 204. Transverse section of the stem showing continuous geo-perceptive layer S; enlarged view, S', of cell of endodermis containing group of large starch-grains (Bryophyllum).

In all the specimens examined, the experimentally located geo-perceptive layer was found to coincide with

the 'starch-sheath.' The statolith-theory thus obtains strong support from an independent line of experimental investigation. The statolith-theory has been adversely criticised because in simpler organs geotropic action takes place in the absence of statoliths. There is no doubt that the weight of other cell-contents may in certain cases be effective in geotropic stimulation; it may nevertheless be true that 'at a higher level of adaptation the geotropically sensitive members of the plant-body are furnished with special geotropic sense-organs—a striking instance of anatomico-physiological division of labour.'[1]

As previously stated, the electric response in different layers can be successfully detected in vigorous specimens at the proper season. Under less favourable conditions the sensitivity may be found to have disappeared.

Evidence of Insensitive Specimens

I describe the various physico-chemical concomitants which accompany the condition of relative insensibility. I employed three different tests—the electric, the geotropic, and the microscopic—by which the sensitive could be distinguished from the insensitive condition.

Experiment 183. *Electric test.*—Later in the season the geo-electric indications given by the various plants were found to have almost disappeared. That the tonic condition of the specimen was below par was independently revealed by the response to the prick of the probe; this, in vigorous specimens, evokes an electric response of galvanometric *negativity*. But the response to prick in subtonic specimens is quite different, being one of galvanometric *positivity*. The prick-effect, in fact, often gave me an indication as to the suitability of the particular specimen for the observation of geo-electric response.

Experiment 184. *Test of geotropic reaction.*—I took four different insensitive specimens of Bryophyllum and

[1] Haberlandt, *ibid.* p. 597.

Nymphaea, and held them horizontal. Shoots of these plants had, earlier in the season, exhibited very strong geotropic reaction, the stem curving up through 90° in the course of 10 hours or less. But these specimens, obtained later in the season, exhibited very feeble curvature, which hardly amounted to 10°, even after prolonged exposure to geotropic stimulation for 24 hours.

Experiment 185. *Test of microscopic examination.*—I next made sections of the insensitive specimens of Bryophyllum and Nymphaea, and on examining them under the microscope discovered a striking difference. A few weeks before, the groups of large starch-grains stained with iodine were the most striking feature of the starch-sheath. But now these starch-grains could not be found in any of the numerous specimens examined. This is evidence that the presence of the starch-grains is associated with the sensitiveness of the perceptive layer.

Localisation of Geo-Perceptive Layer in Various Plants

The geo-perceptive layer of a large number of plants was similarly localised by the probe, a short account of which is given below.

Commelina.—The geotropic sensibility of the stem of this plant is shown by the erectile movement from a horizontal position. The geo-electric response at the surface was 0. At 0·10 mm. it was −6, which increased to a maximum of −18 at a depth of 0·20. After this the response underwent a rapid decline. The maximally excited layer was subsequently found to contain the starch-grains.

Myosotis.—The stem of Forget-me-not also gave strong geo-electric response, the maximum excitation occurring at a depth of 0·20 mm. In the microscopic section the starch-containing layer was also found at the depth of 0·20 mm.

Centaurea.—The flower-stalk of the Cornflower was

found to exhibit electric response of moderate intensity under the stimulus of gravity. It is sensitive whilst the flower-buds are still closed, but insensitive after the opening of the flower. The maximally excited layer was at a depth of 0·3 mm., which also contained the starch-grains.

Tiger Lily.—The flower-bud of this plant is strongly geotropic. It gave the maximum geo-electric response at a depth of 0·3 mm. The starch-grains occurred very near this layer.

Convolvulus.—This gave the maximum geo-electric response at a depth of 0·3 mm. from the surface, and the starch-layer was found at 0·28 mm. below the surface.

The table given below embodies the results obtained with different plants. Though the maximal excitation occurs at unequal depths in different species of plants, the maximally excited layer is found to coincide with the starch-sheath.

TABLE XXV.—GEO-ELECTRIC RESPONSE AT VARIOUS DEPTHS IN DIFFERENT PLANTS.

Specimen	Galvanometric negativity at depths in mm.											Position of starch-sheath at depth of
	0·0	0·1	0·2	0·3	0·4	0·5	0·6	0·7	0·8	1·4	1·6	
Commelina	0	6	**18**	2	0	...	...	...	...	...	...	0·21
Myosotis	15	27	**80**	31	7	5	0	...	...	...	...	0·20
Centaurea	0	10	22	**40**	8	7	0	...	...	...	...	0·30
Tiger Lily	7	11	25	**54**	7	5	3	...	...	...	...	0·30
Convolvulus	0	5	13	**33**	20	5	0	...	...	...	...	0·28
Bryophyllum	0	...	24	...	45	...	**63**	...	41	3	0	0·60
Nymphaea	1[illegible]	...	26	...	40	...	59	...	92	**108**	72	1·40
Tropaeolum (petiole)	0	6	**25**	2	0	...	...	...	...	...	...	0·2[illegible]

DUPLICATION OF GEO-PERCEPTIVE LAYER

The experiments described above brought out the definite fact that during the passage of the probe from the surface to the centre, it encounters a particular starch-layer, at which the geo-electric response is at its maximum. From

this it might at first appear that the geo-perceptive layer must always be single. There is, however, an interesting variation which is described below.

Experiment 186.—While experimenting with a specimen which was supplied from a nursery garden as the Cape Marigold (a species of Calendula), I was at first greatly puzzled by the fact that this stem exhibited two definite electric maxima during the passage of the probe from the surface to the pith. Thus in a given specimen, while the geo-electric response of galvanometric negativity at a depth of 0·10 mm. was − 60 divisions, it increased abruptly to − 115 divisions at 0·20 mm., and declined to − 15 at the greater depth of 0·30 mm. The response continued to decline till a depth of 0·60 was reached, when the response exhibited a second maximum, this time of − 105 divisions. Below this the excitatory reaction showed decline and abolition. Detailed results are given in the following table:

TABLE XXVI.—SHOWING DUPLICATION OF GEO-PERCEPTIVE LAYER.

Distance from surface	Geo-electric response
Surface 0 mm.	− 10 divisions
0·10 mm.	− 60 ,,
0·20 ,,	− 115 ,,
0·30 ,,	− 15 ,,
0·40 ,,	− 14 ,,
0·50 ,,	− 14 ,,
0·60 ,,	− 105 ,,
0·70 ,,	12 ,,

The two starch-sheaths occurred at depths of 0·15 and 0·58 mm.

Similar duplication of the geo-electric maximum was also observed in a second specimen of the same plant. On examining sections of the stem, it was a matter of great surprise to find that there were two definite starch-layers separated from each other by a distance of about 0·4 mm.: it was at these starch-sheaths that the maximum excitations were observed.

These results afford another striking demonstration of the fact that the layer which contains the starch-grains becomes the focus of excitation when the organ is geotropically stimulated by change from the vertical to the horizontal position.

Another significant fact was noticed in the case of Calendula. Its geotropic excitability was very marked at the beginning of its proper season, but disappeared later. Microscopic sections showed that this insensitive condition was associated with the disappearance of the starch-grains from the two layers. Of these, the starch-grains in the layer nearer the centre were the first to disappear.

Summary

The distribution of excitation induced in an organ under the stimulus of gravity may be mapped out by means of the exploring Electric Probe.

The induced galvanometric negativity of the upper half of an organ (indicative of excitation) shows variation in different layers of the organ. The excitatory reaction attains a maximum value at a definite layer, beyond which there is a decline.

The geo-perceptive layer is experimentally localised by measuring the depth of intrusion of the probe at which maximum deflection of galvanometric negativity occurs.

The geo-perceptive layer thus determined is found to be at or near the starch-sheath which contains a number of large-sized starch-grains.

In certain plants the distribution of geotropic excitability exhibits two maxima: that is, the focus of excitation is not single but double. Microscopic sections showed that the starch-sheath in these is double, and that the positions of the two electric maxima coincide with those of the two starch-sheaths.

The activity of geo-perception undergoes seasonal variation. It declines with the growing subtonicity of the

plant; such specimens exhibit positive electric response under the stimulus of prick, and feeble curvature under geotropic stimulation. The large-sized starch-grains, normally observed in the starch-layer, are found to have disappeared in specimens which prove to be geotropically insensitive.

The induced electric variation in a horizontal organ, negative in the upper, positive in the lower, half, indicates that the cortex contiguous to the upper perceptive layer undergoes contraction, while that contiguous to the lower perceptive layer undergoes expansion.

CHAPTER XXXI

RELATION BETWEEN ANGLE OF INCLINATION AND GEOTROPIC EXCITATION

If the pressure of heavy particles on the sensitive ectoplasmic layer of the cell be the efficient cause of stimulation by gravity, it would follow that the excitation caused by them will increase with the angle of inclination. The following experiments were carried out by the Method of Vertical Rotation, the effect of which is somewhat different from that of Axial Rotation described in a previous chapter. There is no effective stimulation in the vertical position of the plant, while it is most intense at an inclination of 90°. The effective pressure on the protoplasm of the perceptive cell which stimulates it, will evidently increase with the angle of inclination to the vertical. The problem to be solved is the exact determination of the relation between the angle of inclination and the associated excitation.

As regards the measurement of the induced excitatory reaction, it is theoretically possible to determine it from either mechanical or the electric response at various inclinations. The practical difficulties in the measurement of the mechanical response are, however, so numerous, that it is impossible to obtain with it any sufficiently accurate result. No such difficulties are encountered in the electric method, the relative advantages of which are as follows:

1. The latent period is very short and the maximum excitatory reaction is attained in the course of a minute or so;

2. The excitatory reaction of galvanometric negativity disappears on the return of the specimen to the vertical position; and, finally,
3. The errors caused by the inaccurate reading of the angular scale and the physiological asymmetry of the organ may be eliminated by the Method of Reversal. When the plant is inclined to the right through $+90°$, the current of response flows in one direction; when it is inclined to the left through $-90°$, the direction of the responsive current is reversed; the experimental error of a single determination is eliminated by taking the mean of the two galvanometric deflections.

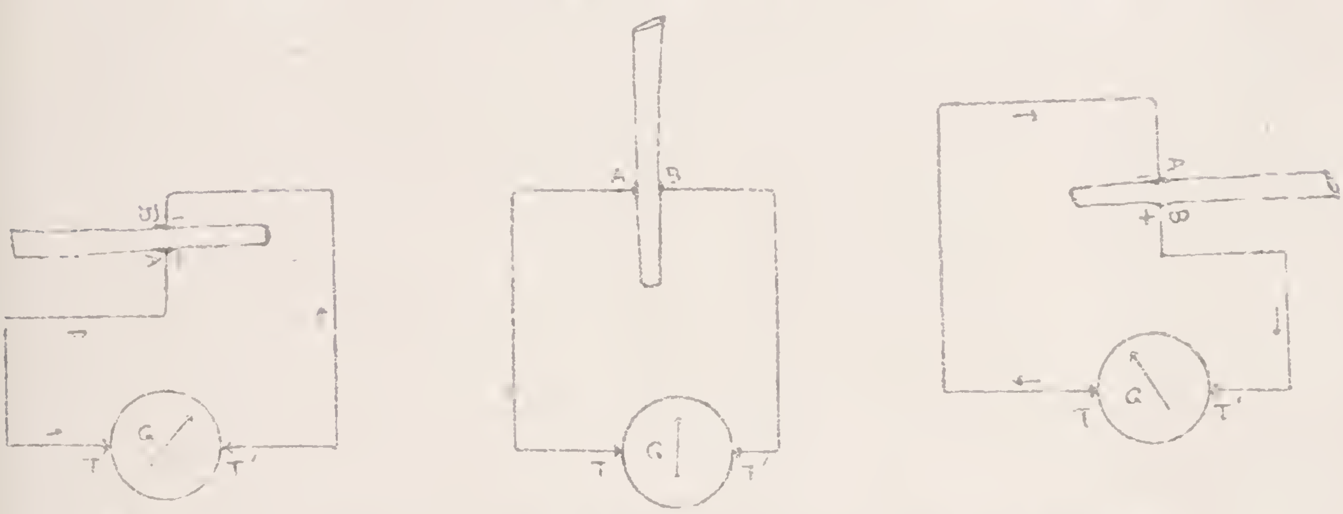


FIG. 205. Diagrammatic representation of inducing the geotropic reaction of the shoot by the Method of Reversal. Rotation through $+90°$ (right) makes A negative, while rotation through $-90°$ (left) renders A positive.

The details of the procedure will be understood from the diagram given in fig. 205. The specimen is at first vertical, with the two symmetrical contacts on its sides A and B, the electrodes being connected in the usual manner with the terminals T T′ of the indicating galvanometer; after rotation through $+90°$ the upper side A becomes excited and galvanometrically negative (right-hand figure). The specimen is next rotated to $-90°$; A now becomes the under, and B the upper and excited, side (left hand figure). The electromotive response is now reversed, B being galvanometrically negative. The induced electromotive

variation thus obtained is of considerable intensity, often exceeding 15 millivolts.

Excitatory reaction at 45° and 90°.—The special difficulty encountered is that of the accurate determination of the angle of inclination. An index is attached to the plant, and a stationary circular scale permits the determination of the angle at which the plant is inclined to the vertical. But

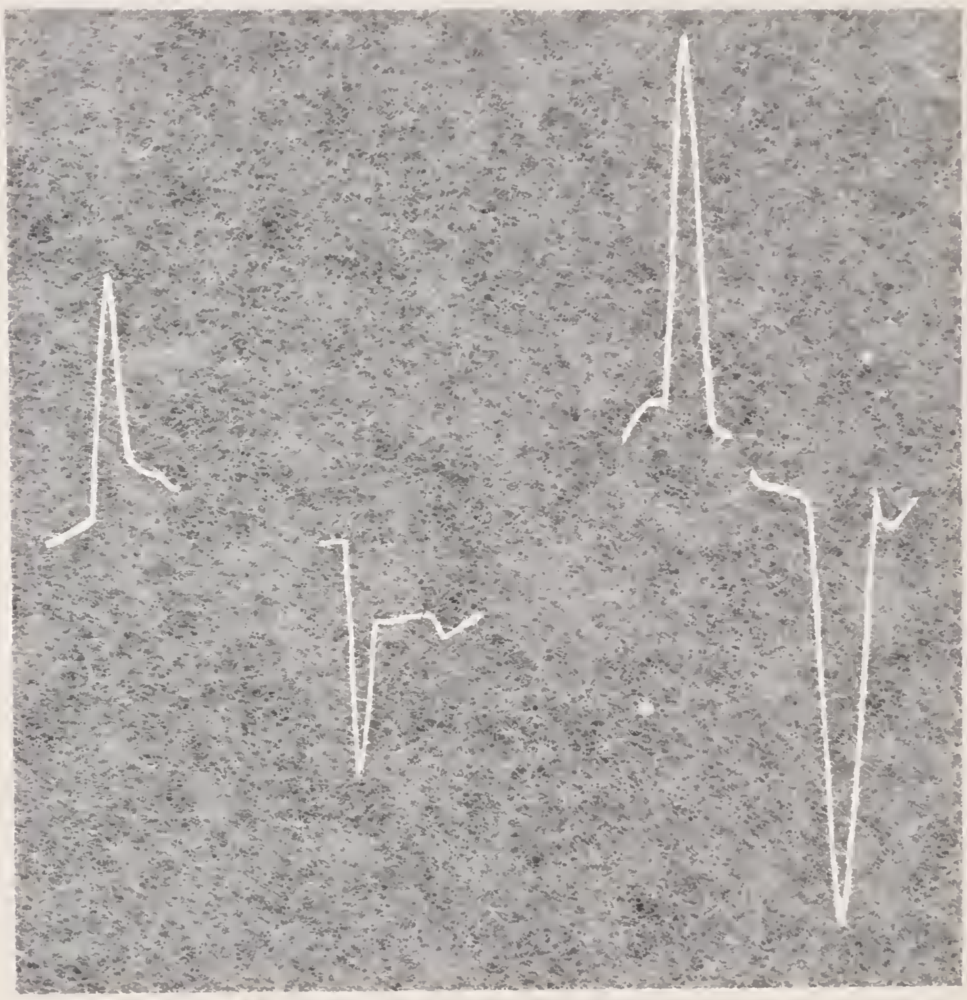


FIG. 206. Alternate geo-electric reactions at + 45° and − 45°, also at + 90° and − 90° (Method of Vertical Rotation).

the vertical or zero-reading itself is subject to an error of a few degrees, which is accentuated by the fact that the perceptive layer inside the plant may not be exactly parallel to the surface of the stem or the petiole. The only means of eliminating the error is by taking two responses, say at + 45° and − 45°, by the Method of Reversal. The mean of the two responses obtained through successive positive and negative rotations of the specimen will reduce or eliminate all errors.

Experiment 187.—I obtained a series of galvanometric responses with a petiole of Tropaeolum when rotated through the entire cycle of inclination from the vertical to 45° (as read by the movement of the index), back to zero and then to − 45°, and back once more to zero. The same procedure was followed in the case of inclination at 90°. The records are given in fig. 206; the response to inclination of + 45° is seen as an up-curve, with subsequent recovery on return to the vertical. Inclination of − 45° evoked a reverse response of down-curve, with subsequent recovery. Inclinations of + 90° and − 90° evoked responses of larger amplitude. The ratio of reactions at 90° and 45°, as determined by the amplitude of responses, came out in this case as 1 : 1·5. The ratio of sin 90° : sin 45° is 1 : 1·41.

The following table embodies the reactions observed at 45° and 90° in six different specimens of the petiole of Tropaeolum:

TABLE XXVII.—EXCITATORY REACTIONS AT INCLINATIONS OF 45° AND 90° (PETIOLE OF TROPAEOLUM).

No.	Electric response		Ratio $\frac{b}{a}$
	(a) at 45°	(b) at 90°	
1	37 divisions	55 divisions	1·482
2	28 ,,	40 ,,	1·428
3	192 ,,	274 ,,	1·426
4	22 ,,	32 ,,	1·454
5	31 ,,	44 ,,	1·420
6	37 ,,	53 ,,	1·432
Mean ratio of reactions			1·44
Ratio of sines			1·41

The ratio of excitatory reaction at the two angles is 1·44, while the ratio of the sines is 1·41. It will be noted that there is a persistent small difference between the two ratios, the excitation at the larger angle being greater than the value deduced from the ratio of the sines. The

relatively greater excitation at the larger angle may have a physiological significance, to which reference will be presently made.

Experiment 188. *Excitatory reaction at 45°, 60°, and 90°.*—The excitatory reactions of a different batch of petioles of Tropaeolum were next obtained for the three angles of inclination of 45°, 60°, and 90°.

TABLE XXVIII. EXCITATORY REACTIONS AT ANGLES OF INCLINATION OF 45°, 60°, AND 90° (PETIOLE OF TROPAEOLUM).

No.	Electric response at		
	(a) 45°	(b) 60°	(c) 90°
1	36 divisions	49 divisions	54 divisions
2	32 ,,	40 ,,	47 ,,
3	31 ,,	40 ,,	46 ,,
4	22 ,,	29 ,,	34 ,,
5	14 ,,	19 ,,	25 ,,
6	19 ,,	22 ,,	25 ,,
Mean value	26 ,,	33 ,,	38 ,,

Ratio of reactions . . . . . 1 : 1·28 : 1·47
Ratio of sines . . . . . 1 : 1·22 : 1·41

The determinations given above again show that the excitation is but approximately proportional to the sine of the angle of inclination, the ratio of reactions at the larger angles being relatively greater. Another series of observations was made, the angle of inclination being increased by steps of 10°.

Experiment 189.—The photographic records of the reactions at the successive angles of inclination of 45°, 55°, 65°, 75°, and 90° are reproduced in fig. 207.

Experiment 190.—Further experiments were carried out with twelve different specimens of the petiole of Tropaeolum and the mean excitatory reaction at the different angles are given in the following table :

TABLE XXIX.—EXCITATORY REACTION AT VARIOUS ANGLES

Angles . . .	45°	55°	65°	75°	90°
Response . . .	40·3 divs.	47 divs.	[illegible]	60·5 divs.	[illegible]
Ratio of reactions . .	1 :	1·15 :	1·34 :	1·48 :	1·55
Ratio of sines . .	1 :	1·16 :	1·28 :	1·36 :	1·41

The ratio of reactions, compared with the ratio of sines, is hence seen to undergo a gradual increase with increasing angle of inclination. Thus, to take the two extreme

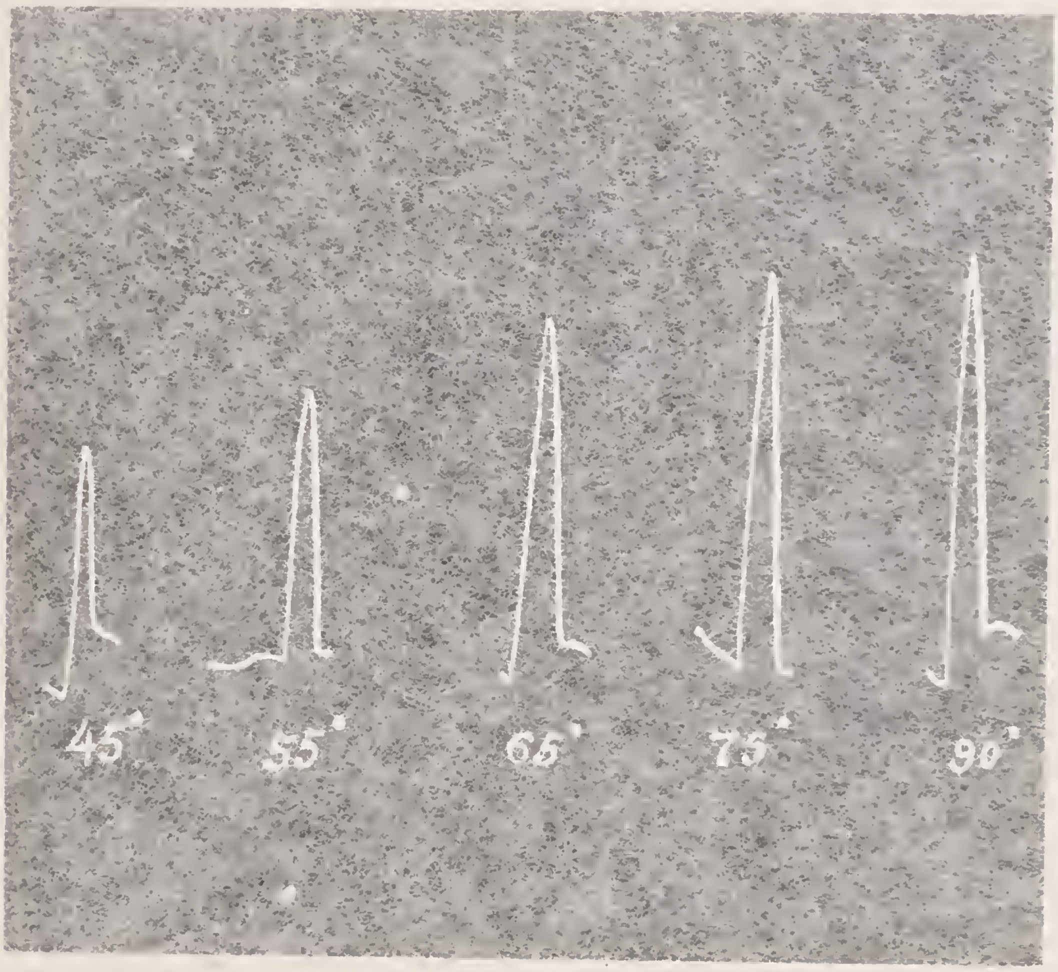


Fig. 207. Records of geo-electric response at various angles (Tropaeolum).

cases, the divergence between the two ratios at 55° is 2·6 per cent., whereas at 90° it is 9 per cent. This definite divergence, which is persistent in all determinations, points to some physiological difference.

In attempting to find an explanation of the relatively greater reaction at the larger angles of inclination, it is necessary to take account of two distinct factors in the

sensitive cells; first, the pressure exerted by the particles, and, second, the irritability of the ectoplasmic layer pressed upon by the particles. As regards the first, the effective pressure exerted by the particles is proportional to the sine of the angle of inclination; but in regard to the second, the irritability of the ectoplasmic layer may not be the same throughout the length of the cell, but be greater towards the apical end. At the smaller angle of inclination, say to the right, the statoliths, originally at the base of the cell, accumulate at the right-hand lower corner of the cell, a portion of the basal end of the cell being thus subjected to pressure. When the angle of inclination is increased, the statoliths come to lie along the whole lateral length of the cell, extending to the apical end. The relatively greater excitation with increasing angle of inclination may therefore be explained on the assumption that the excitability of the ectoplasm is greater towards the apex; facts will be given which appear to lend support to this view.

Excitatory Reaction at 45° and 135°

Controversy has arisen over the question as to whether the intensity of geotropic excitation is the same or different at the angles of inclination 45° and 135°. The effective pressure exerted by the stimulating particles in the cells is the same at the two angles; the only difference in the two cases is the collection of the particles at the basal end of the cells at 45°, and at the apical end at 135°. Czapek found that the effective stimulus of gravitation is greater when the organ is held at 135° than when it is held at 45°, though his results have not been accepted by others.

I carried out investigations on the subject, employing the method of electric response. Allowance was made for any possible change in excitability brought on by fatigue. This was secured by conducting the experiments in the following sequence of observation: (1) reaction at 45°; (2) reaction at 135°; and (3) reaction once more at 45°. The comparison of the first and the third responses showed

whether any change in excitability had occurred on account of fatigue, allowance for which was made by taking the mean of the two responses for 45° at the beginning and at the end of the series.

Experiment 191. *Geo-electric response at 45° and 135°.*—The following observations were made with the petiole of Tropaeolum: the first and the third responses at 45° were found to be 47 and 45 mm. respectively, the mean of the two being 46 mm. The second or intermediate response, taken at 135°, gave 55 mm. The excitatory reactions at 45° and 135° are thus in the ratio of 46 : 55, or as 1 : 1·2. In a second series with a different specimen, the first and the third responses at 45° were both 25 mm. (fig. 208). There was in this case no fatigue. The intermediate response at 135° was 31 mm. The ratio of the excitatory reactions at the two angles is thus in the proportion of 25 : 31, or as 1 : 1·2. The excitation at 135° is thus about 20 per cent. greater than at 45°.

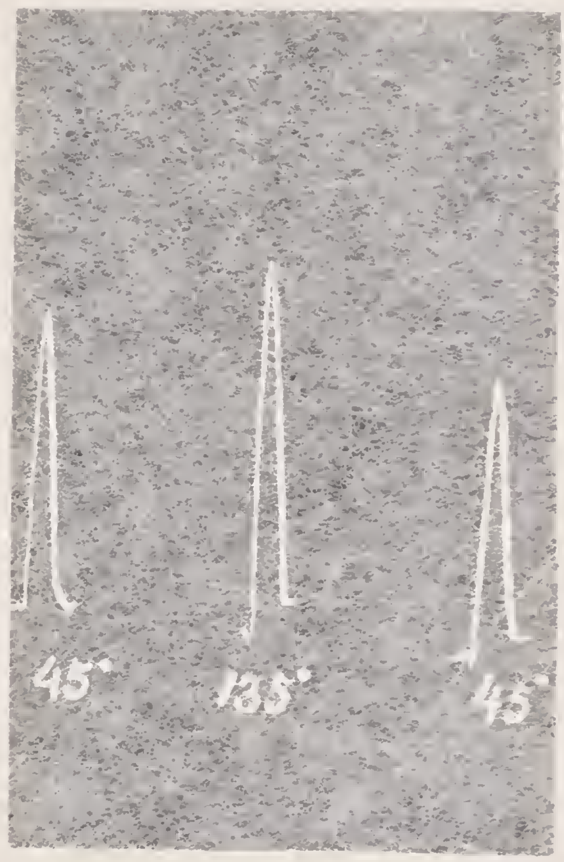


FIG. 208. Geo-electric response at 45°, 135°, and 45° in sequence.

The stem of Convolvulus was employed for the next series of experiments. At 45° the excitatory deflection was 26 divisions; when the angle was increased to 135°, the deflection was enhanced to 31 divisions. That the excitation at 135° was greater than at 45° was evidenced in a convincing manner on return to the angle of 45°, when the galvanometric spot of light was immediately restored to almost the first deflection; there was slight fatigue, and the deflection was 25 divisions instead of the former value of 26 divisions. The ratio of the two reactions at 45° and 135° is thus 25·5 : 31, or 1 : 1·23. In the second series of experiments the two excitatory deflections

were as 18 : 21, or 1 : 1·31, the mean ratio from the two experiments being 1 : 1·27. These various results all tend to show that the excitation is greater at 135° than at 45°. In the following table the readings at 45° are those at the beginning and at the end of the series of observations, the reading at 135° being the intermediate one.

TABLE XXX.—EXCITATORY REACTIONS AT 45° AND 135°.

Specimen	Electric response at		
	45°	135°	45°
Tropaeolum	47 divisions	55 divisions	45 divisions
,,	25 ,,	31 ,,	25 ,,
Convolvulus	26 ,,	31 ,,	25 ,,
,,	16 ,,	20 ,,	16 ,,

Ratio of reactions at 45° and 135° . . Tropaeolum 1 : 1·2
,, ,, ,, ,, . . Convolvulus 1 : 1·27

These very definite results tend to prove that the ectoplasmic layer is not uniformly irritable at all points, but that it is more excitable at the apical end than at the basal end of the cells.

SUMMARY

Geotropic reaction is found to vary approximately with the sine of the angle of inclination.

The results of numerous experiments carried out by the Method of Vertical Rotation tend to show that the excitatory reaction at a large angle of inclination is relatively greater than the value deduced from the law of sines. This suggests the inference that the excitability of the ectoplasmic layer is greater at the apical end of the geo-perceptive cells than at the basal end.

This conclusion is confirmed by the fact that the excitatory reaction at 135° is about 1·2 times greater than that at 45°. At 45° the starch-grains accumulate at the basal, and at 135° at the apical, end of the cells.

CHAPTER XXXII

THE CRITICAL ANGLE FOR GEOTROPIC EXCITATION

THE results of investigations described in the present chapter afford independent evidence that the falling starch-grains are the effective agents in geotropic excitation. The facts to be presently described will be better understood from the following illustration. If some sand-grains be placed on a flat board which is gradually tilted, the particles start sliding down only after a certain critical angle has been reached. If the board is rough, this critical angle will be large; if it is smooth, the angle will be small. Moreover, by the scouring action of the sand, the rough surface may become smoothed down after numerous repetitions of the experiment, the result being a reduction of the critical angle.

If geotropic stimulation is effected by the fall of the starch-grains, it would be expected that:

1. At a small angle of inclination the grains will not be immediately displaced; therefore no excitation will ensue.

2. When the angle of inclination is gradually increased, the grains will slide down as soon as the critical angle is exceeded. This fall of particles and the resulting pressure on the protoplasm will constitute a stimulus and give rise to an excitatory response.

3. The critical angle will probably be lowered to a certain extent, on repetition of the process, by the reduction of frictional resistance to the fall of the particles.

4. Were the weight of the fluid contents of the cell in the higher plants the only means for stimulation by gravity, the excitatory reactions would be proportional to the sines

of all angles of inclination above zero. But if the fall of solid particles be the efficient cause, there will be a hiatus in this relation, for there will be no excitatory response at angles smaller than the critical. Even at a slightly greater angle than the critical, some of the particles may remain adherent, and the excitation will then be disproportionately lower than what is demanded by the law of sines. It is only after the critical angle has been considerably exceeded that the relation of sines will be found to hold good, at least approximately.

The above considerations will now be subjected to the test of experiment to discover, in the first place, if there is any discontinuity in the responsive reactions at angles below 45°.

Excitatory Reaction at 35°, 45°, and 60°

From the results of experiments detailed in the previous chapter it was found, for angles of 45° and 60°, that geo-electric excitation is approximately proportional to the sine of the angle of inclination. In order to observe whether this relation holds good at other angles, a series of observations was made with six different specimens of the petiole of Tropaeolum at 35°, 45°, and 60°. The results are given in the following table:

Table XXXI.—Excitatory Reactions at 35°, 45°, and 60°

Specimen	Electric response		
	35°	45°	60°
1	19 divisions	30 divisions	[illegible] divisions
2	19 ,,	32 ,,	42 ,,
3	7 ,,	31 ,,	40 ,,
4	7 ,,	22 ,,	29 ,,
5	5 ,,	14 ,,	19 ,,
6	5 ,,	19 ,,	21 ,,
Mean	10·3 ,,	20·1 ,,	33·1 ,,

From these figures it appears that on increasing the angle beyond 45°, the ratio of reactions at 60° and 45° is as 1·27:1, while the ratio of sines of 60° to 45° is as 1·22 : 1.

On decreasing the angle, on the other hand, the ratios are the following

Ratio of reactions at 45° and 35° is as 1 : 0·39
,, sines of 45° ,, 35° ,, 1 : 0·81

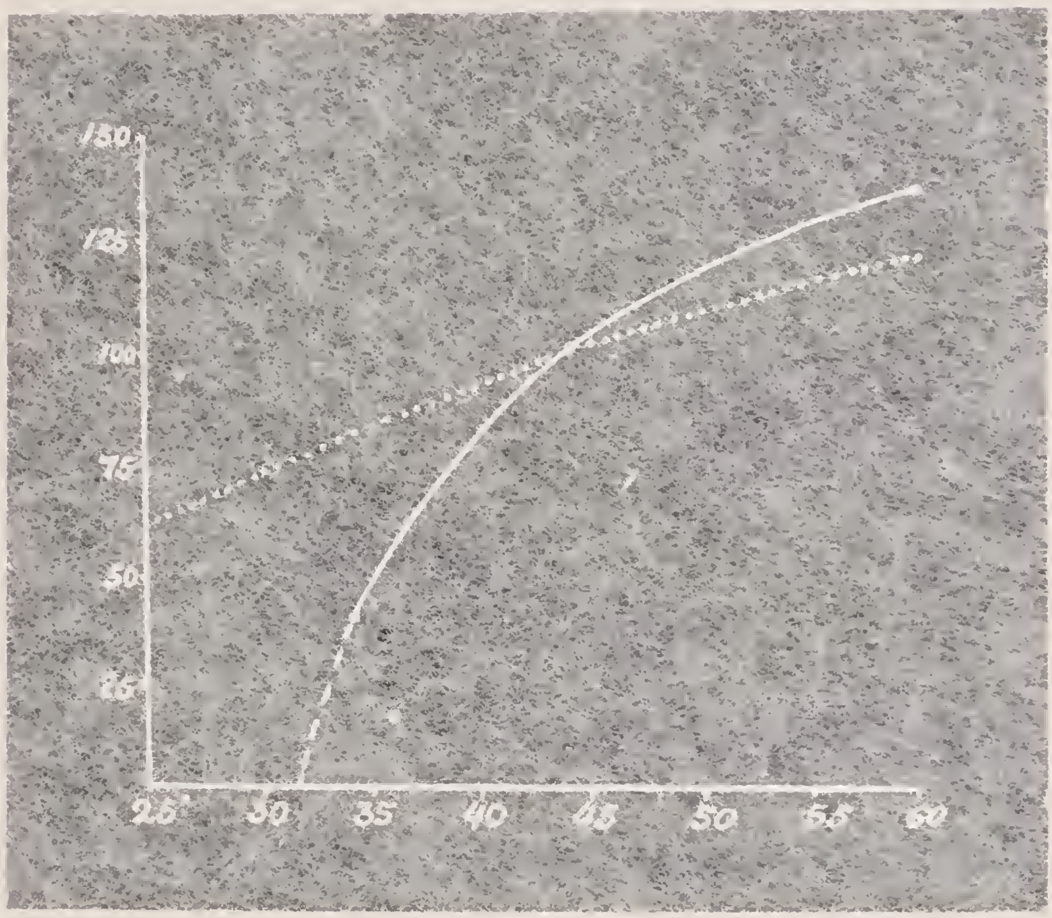


FIG. 209. Curves showing values of sines (dotted) and of reactions (thick line). The latter produced cuts abscissa at 31·5°, indicating absence of excitation at a critical angle. (Ordinate represents reaction, abscissa the angle of inclination. (Tropaeolum.)

The reaction at smaller angles is thus found to be disproportionately lower.

Multiplying the above ratios by 100, in order to avoid decimals, they become :

	35°	45°	60°
Reactions	39	100	127
Sines	81	100	122

The relation between angle of inclination and resulting reaction above and below 45°, found from the results just given, is shown in fig. 209 ; the dotted curve represents

the sines of the various angles of inclination; the continuous line represents the excitation at the corresponding angles. It will be noticed that while the divergence between the sines and the reactions is not excessive above 45°, it is very pronounced at the smaller angle of 35°; it indicates the approach of some hiatus or discontinuity. On producing the curve backwards it intersects the abscissa at or about 31·5°, at which angle the excitation would appear to be reduced to zero. This is the critical point; beyond this angle the excitatory reaction should be abrupt.

It remains now to ascertain whether such a critical point does actually exist.

Determination of the Critical Angle

The discovery of the critical angle was the outcome of my investigations on the geo-electric response of Nymphaea (1919). The electric response recorded was that given on inclining the specimen from the vertical to the horizontal. This was done very gradually in order to avoid any mechanical disturbance likely to disarrange the electric contacts. There was at first no indication of geotropic excitation as the angle was gradually increased from zero, and it was a matter of astonishment to note the reaction which occurred abruptly when the inclination reached the approximate value of 33°. The excitatory reaction was exhibited by the sudden deflection of the hitherto quiescent galvanometer spot of light. On return to the vertical position the excitatory deflection disappeared. Repetition of the experiment gave practically the same result. The only explanation for this unexpected phenomenon is that geotropic excitation is caused by the abrupt fall of heavy particles in the perceptive cells, when the inclination exceeds the critical angle.

It is necessary at this point to define the critical angle; it is the angle of inclination at which the excitatory geotropic reaction is abruptly manifested. This, as already

explained, can be reasonably attributed to the sudden fall of heavy particles on to the sensitive protoplasm of perceptive cells. Displacement of the particles will no doubt occur even at a smaller angle of inclination, but only *after a considerable length of time*, the displacement being helped by protoplasmic movement; whereas at the critical angle the excitatory reaction will be *immediate*. It is very remarkable that the critical angle in the case of Nymphaea should be so near the theoretical value of 31·5°. The critical angle of 33° found for Nymphaea was a rough approximation. The following experiments were carried out for the determination of the critical angle in various plants, every precaution being taken for ensuring the highest accuracy.

FIG. 210. Abrupt geo-electric response at an inclination of 31° (Tropaeolum).

Experiment 192. *Determination of the critical angle for the petiole of Tropaeolum.*—I give a photographic record of the electric response of the petiole of Tropaeolum as its inclination was gradually increased from 25° to 31°, by successive steps of 2°. There was no response at 25°, 27°, and 29°. When the inclination reached 31°, response occurred abruptly (fig. 210). Restoration of the organ to the vertical was attended by recovery.

The possible error in the exact setting of the index at zero of the scale is eliminated by observing the effects of alternate inclinations to the right and to the left. The mean of the two effective angles of inclination thus gives the true value of the critical angle.

Experiment 193. *Exact determination of the critical angle for the petiole of Tropaeolum.*—The angle of inclination

to the right was gradually increased, and the hitherto quiescent spot of light exhibited a sudden deflection to the right at 30°. On return to the vertical the excitatory reaction disappeared. Inclination to the left gave a sudden deflection to the left at − 35°. The critical angle is therefore 32·5°.

Experiment 194. *Determination of the critical angle for the stem of Tropaeolum.*—The critical angle for the stem was next determined, the procedure adopted being the same as in the last case. The minimum angle at which response occurred to right-handed rotation was 33°: rotation to the left elicited reaction at − 30°. Hence the true critical angle for the specimen was 31·5°. Five other determinations were made with other specimens, and the mean critical angle obtained was 32·7°, which is very nearly the same as the critical angle for the petiole.

Experiment 195. *Critical angle for the stem of* Commelina bengalensis.—With this plant an inclination of 30° to the right induced the excitatory reaction: inclination in the opposite direction induced reaction at − 33°. The true critical angle is thus 31·5°. In a second specimen the mean value of the critical angle was found to be 31°.

TABLE XXXII.—THE CRITICAL ANGLE FOR VARIOUS PLANTS.

Specimen	No.	Inclination to right and left		Critical angle in degrees	Mean
Petiole of Tropaeolum	I.	30	− 35	32·5	31·8
	II.	30	− 34·5	32·25	
	III.	35	− 30	32·5	
	IV.	29	− 32	30·5	
	V.	31	− 32	31·5	
Stem of Tropaeolum	I.	33	− 30	31·5	32·7
	II.	35	− 30	32·5	
	III.	36	− 30	33·0	
	IV.	35	− 32	33·5	
	V.	34	− 33	33·5	
	VI.	33	− 30	31·5	
Stem of Commelina	I.	30	− 33	31·5	31·25
	II.	32	− 30	31·0	

The mean critical value for all the various plants examined is 31·8°, the maximum variation from this is less than 1°. It is very remarkable that the critical angles for different plants should exhibit so close an agreement.

The Effect of Repetition

Experiment 196.—It was stated at the outset that repetition of the experiment might reduce the friction and diminish the critical angle. It is very interesting that this should have been found to be actually the case. I took three different specimens of the petiole of Tropaeolum, the experiments being carried out three times in succession. In every case it was found that the effect of repetition was to produce a not inconsiderable lowering of the critical angle. In the first specimen the critical angle was lowered from 32·5° to 28·5°, in the second from 31° to 22·5°, and in the third from 30° to 22·5°.

Table XXXIII.—The Effect of Repetition on the Critical Angle.

Specimen	Sequence of repetition	Direction of inclination		Mean critical angle
		Right	Left	
I. Petiole of Tropaeolum	1	30	35	32·5
	2	30	32	31
	3	27	30	28·5
II. Petiole of Tropaeolum	1	30	32	31
	2	25	28	26·5
	3	20	25	22·5
III. Petiole of Tropaeolum	1	29	31	30
	2	24	30	27
	3	20	25	22·5

These experiments offer a very strong confirmation of the statolithic theory. The fact that when the organ is gradually inclined from the vertical there is no excitation till the critical

angle is reached, and that then there is an abrupt excitatory reaction, can only be satisfactorily explained on the theory of the sudden fall of heavy particles from the base on to the side of the perceptive cells.

Summary

The excitatory reaction under the stimulus of gravity is reduced disproportionately with the diminution of the angle of inclination. This indicates the approach of some hiatus or discontinuity. By producing the curve of excitation backwards, it cuts the abscissa at about 31·5°, at which angle the abrupt excitatory reaction should be reduced to zero.

The critical angle for geotropic excitation has been found in a large number of plants to be about 31·8°.

The effect of repetition of inclination is found to lower the critical angle.

The abrupt excitatory reaction induced beyond the critical angle can only be attributed to the sudden fall of heavy particles from the base on to the side of the sensitive cells.

CHAPTER XXXIII

THE RESPONSE OF THE ROOT TO DIFFERENT STIMULI

THE electric response of the *shoot* to the stimulus of gravity has been described in previous chapters; it was shown that its response to geotropic stimulation is similar to that to other modes of stimulation.

The response of the *root* to stimulation of various kinds will be described in the present chapter. It should be borne in mind that the responsive curvature in the root takes place in the sub-apical growing zone which is separated by a certain distance from the tip. Stimulation is therefore direct only when the stimulus is applied at the responding growing region; it is indirect when applied at the tip. The intervening distance between the root-tip and the responsive zone of growth is semi-conducting.

I may briefly recapitulate the effects of indirect and direct stimulation as exhibited by mechanical response of the root described in greater detail in a previous chapter.

Effect of unilateral stimulation of the root-tip.—Stimulation of the tip induces indirect stimulation of the growing region higher up on the same side. The resulting expansion produces a *negative* curvature away from the stimulated side. This occurs under modes of stimulation as diverse as photic and thermal. It has been shown that this effect is not peculiar to the root but also occurs in the shoot as the consequence of indirect stimulation of the growing region (p. 142).

Effect of direct unilateral stimulation of the growing region.—In contrast with the negative curvature induced

by indirect stimulation, direct unilateral stimulation of the growing region gives rise to a positive curvature (p. 143).

I now go on to describe the electric response resulting from (1) indirect stimulation of the root-tip, and (2) direct stimulation of the growing region.

Electric Response to Indirect Stimulation

Experiment 197.—One of the two electric connections with the galvanometer is made at a point A (*see* fig. 211) on one side of the growing region of the root of the Bean (*Vicia Faba*), the other connection being made at the diametrically opposite point B. Unilateral stimulation was applied at the root-tip *a*, and on the same side as A. The tip was subjected to various modes of unilateral stimulation; mechanical stimulation was effected by friction with emery-paper, or by pin-prick; chemical stimulation was produced by application of dilute hydrochloric acid; thermal stimulation was effected by the proximity of an electrically heated platinum wire. In every case the response was that of induced galvanometric positivity at A. The electric variation took place within about 10 seconds of the application of stimulus; the time-interval obviously depends on the length of path to be traversed by the transmitted impulse causing indirect stimulation.

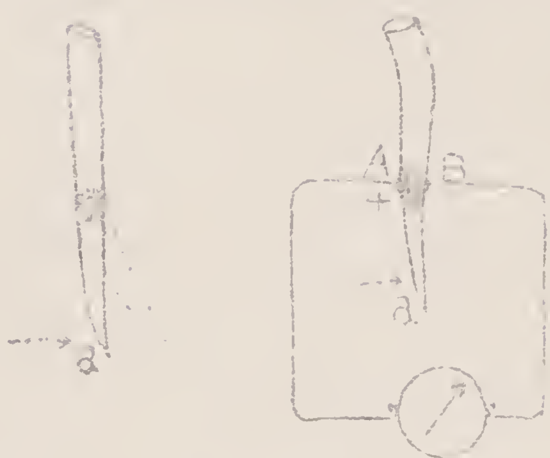


FIG. 211. Diagrammatic representation of mechanical and electric response of root to indirect stimulation, the stimulus having been applied at the tip *a*. Figure to the left shows responsive mechanical movement away from the stimulus. The electric response to indirect stimulation is indicated in the figure to the right, the point on the same side exhibiting galvanometric positivity at A. The shaded part indicates the responsive region of growth at some distance from the tip. (*Vicia Faba*.)

The galvanometric positivity at A gave indication that there was an increase of turgor and expansion induced at

that point, in consequence of which the organ would curve away from the stimulus. Thus the mechanical and electric methods of investigation both lead to the identical conclusion that unilateral stimulation of the tip of the root gives rise to a movement such that the organ recoils from the source of stimulation; since tropic movement towards the stimulus is termed positive, this opposite response must be termed negative.

TABLE XXXIV.—EFFECT OF UNILATERAL STIMULATION OF THE ROOT-TIP

Effect at the proximal side A in the growing region	Effect at the distal side B
Galvanometric positivity, indicative of increase of turgor and expansion	Negligible
The corresponding tropic curvature is negative, *i.e.* a movement away from stimulus.	

A similar electric method was employed for the detection of geotropic excitation in the root, both at the root-tip and at the zone of growth in which geotropic curvature is effected. The two diametrically opposite contacts at the tip will be distinguished as *a* and *b*, the corresponding points higher up in the growing region being A and B (*cf.* figs. 212, 215). When the root is vertical the electric conditions at the two diametrically opposite points are practically the same. But when the root is rotated in a vertical plane through 90° a geo-electric response is found to take place; the responsive current disappears when the root is brought back to the vertical. Rotation through −90° gives rise to a responsive current in the reverse direction.

GEO-ELECTRIC RESPONSE OF THE ROOT-TIP

Experiment 108.—I took the root of a Bean (*Vicia Faba*) and made two electric contacts at two diametrically opposite points, *a* and *b* (*see* fig. 212), on the root-tip at a distance of about 1·5 mm. from the extreme end. Owing

to the very small size of the tip, this is by no means an easy operation. Two platinum points tipped with kaolin paste are very carefully adjusted so as to make good electric contacts at the two opposite points, without exerting undue pressure. The root has to be laid horizontal for geotropic stimulation, and as the root of the Bean is somewhat long and limp, displacement from the vertical position is apt to cause a break of the electric contact. This is avoided by

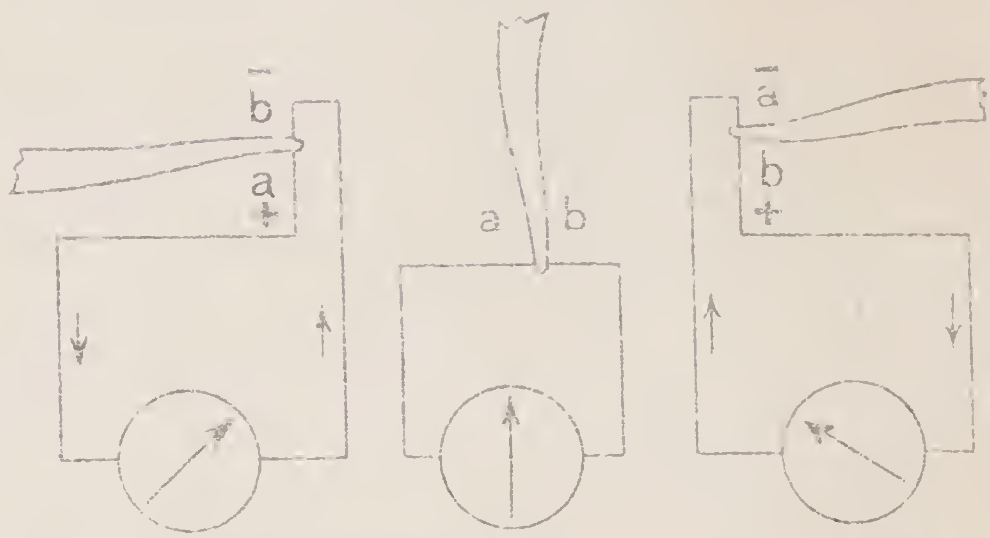


FIG. 212. Diagrammatic representation of geo-electric response of root tip. The middle figure shows root in vertical position. Rotation through $+90°$ places *a* above which becomes galvanometrically negative. Rotation through $-90°$ places *b* above and makes it negative.

supporting the root from the top and also from the sides with padding of cotton-wool.

After due observance of these precautions, the electric response obtained is found to be very definite. When the root is made horizontal by rotation through $+90°$, the point *a* is above, and the responsive current is found to flow from *b* to *a*, *the upper side of the tip* becoming galvanometrically negative; when the root is brought back to the vertical, the responsive current disappears. Rotation through $-90°$ now makes the point *b* occupy the upper position, and the responsive current is from *a* to *b*. Hence the upper side exhibits in every case an excitatory electric change of galvanometric negativity (fig. 212). The root-tip thus gives the characteristic response to direct stimulation. Experiments carried out with twelve different

specimens gave concordant results. The following table gives the absolute values of electromotive force induced at the tip under geotropic stimulus in three different specimens.

TABLE XXXV.—GEO-ELECTRIC RESPONSE OF THE ROOT-TIP (*Vicia Faba*).

Specimen	Induced E.M.F.
1	0·0011 volt
2	0·0010 ,,
3	0·0015 ,,

ELECTRIC RESPONSE IN THE GROWING REGION

Experiment 199.—Investigation was next undertaken on the electric variation induced in the growing region under the stimulus of gravity. The experimental difficulties are here less serious, since the available area of contact for galvanometric connection is not so restricted as in the case of the root-tip. The specimen was securely mounted so that the root was vertical. It was then rotated through $+90°$ into the horizontal plane, so that the point A (*see* fig. 213) in the growing region occupied the upper position. The electric response in the growing region was very definite and took place in a short time. The induced electric change at A was one of galvanometric *positivity* indicative of increase of *turgor and expansion*.

The next series of experiments was carried out in the following order. The root was first rotated through $+90°$ so that A was above. The responsive electric variation, as already stated, was galvanometrically *positive*. The root was then rotated back to the vertical position when the current disappeared. The root was next rotated through $-90°$ and the responsive current became reversed, the now upper point B having become electro-positive. Alternate rotations through $+90°$ and $-90°$ were carried out six times in succession with consistent results. The interval allowed between one stimulation and the next was determined

by the period of complete recovery. Growing fatigue was found to increase this period; at first it was 7 minutes, at the second repetition it was 10 minutes, and at the third time it was prolonged to 15 minutes.

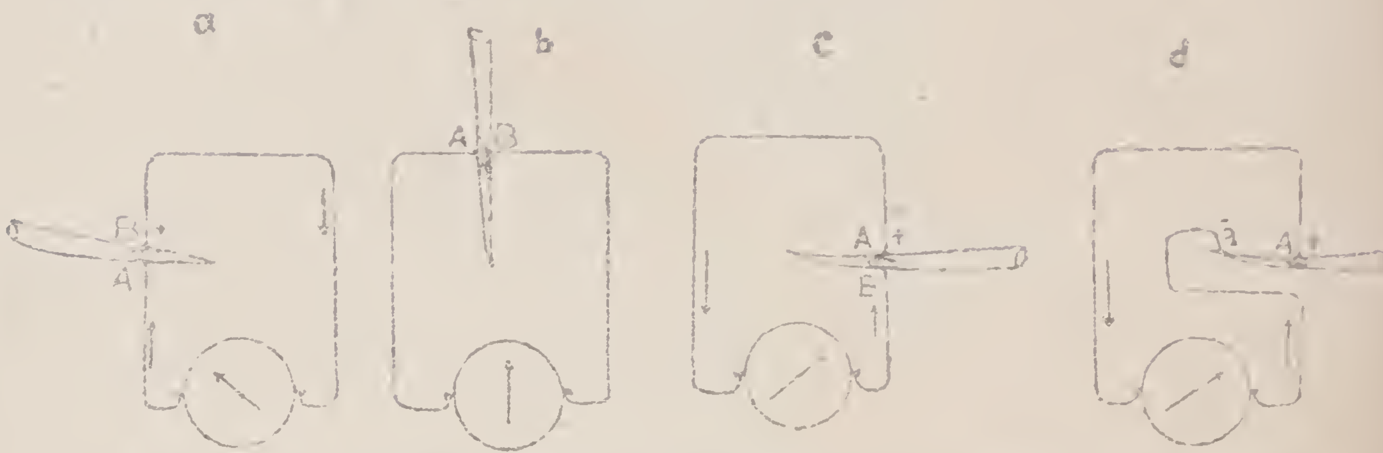


FIG. 213. Diagrammatic representation of geo-electric response in growing region of root.

a, rotation through $-90°$ makes B galvanometrically positive. *b*, vertical and neutral position. *c*, rotation through $+90°$ places A above and renders it galvanometrically positive. *d*, additive effect on current of response, root-tip *a* negative and growing region A positive.

I give below the series of electric responses induced by alternate rotation through $+90°$ and $-90°$. The upper position was occupied by A in the odd series, and by B in the even series. In every case the upper side became galvanometrically positive.

TABLE XXXVI.—GEO-ELECTRIC RESPONSE OF ROOT IN THE REGION OF GROWTH.

Odd series	Galvanometer deflection A, positive	Even series	Galvanometer deflection B, positive
1	20 divisions	2	18 divisions
3	16 ,,	4	18 ,,
5	10 ,,	6	12 ,,

ADDITIVE ACTION-CURRENT AT THE TIP AND AT THE GROWING REGION

It has been shown that under geotropic stimulation the upper side of the tip *a*, being directly stimulated, becomes galvanometrically negative; while the indirectly

stimulated point A, in the growing region higher up, becomes galvanometrically positive. If now two galvanometric connections be made at the points *a* and A, the induced electric difference is increased and the galvanometric response becomes enhanced.

Experiment 200.—The root was at first held vertical, and two electric contacts made at *a* and A. In this neutral position there is little or no current. But as soon as the root was laid horizontal, an electromotive response was exhibited which showed that *a* was galvanometrically negative and A galvanometrically positive (*see* fig. 213, *d*). The induced electric response disappeared on restoration of the root to the vertical position. I give below the results of typical experiments with a vigorous specimen which gave strong electric response. It was possible to repeat the geotropic stimulation six times in succession, the results being invariably consistent. The responses taken in succession exhibited slight fatigue, the first deflection being 140 divisions, and the sixth 115 divisions, of the galvanometer scale.

TABLE XXXVII.—INDUCED ELECTROMOTIVE VARIATION BETWEEN THE TIP AND THE GROWING REGION (*a* NEGATIVE AND A POSITIVE).

Geotropic stimulation	Resulting electric response
First stimulation	140 divisions
Second ,,	130 ,,
Third ,,	130 ,,
Fourth ,,	123 ,,
Fifth ,,	127 ,,
Sixth ,,	115 ,,

These results lead to the conclusion that under geotropic stimulation:

(1) the induced galvanometric negativity at the upper half of the root-tip is due to direct stimulation; and
(2) the induced galvanometric positivity of the growing region on the same side is due to indirect stimulation by transmitted impulse.

GEO-PERCEPTION AT THE ROOT-TIP

The results given above fully confirm Charles Darwin's discovery that it is the root-tip that perceives the stimulus of gravity; he found that removal of the tip abolished the geotropic response of the root. The objection has been raised that the shock-effect of the operation is itself the cause of abolition of response. But subsequent observations have shown that Darwin's conclusions are in the main correct.

The experiments which have been described on the geo-electric response of the root-tip and of the growing region offer convincing proof of the perception of stimulation at the tip, and of the indirect stimulation of the growing region. These experiments exhibit, in one and the same *uninjured* organ, the excitatory reaction at the upper side of the tip, the cessation of excitation, and the excitation of the opposite side of the tip, following the rotation of the organ through $+90°$, $0°$, and $-90°$. The effect at the growing zone is precisely the opposite to that at the tip, *i.e.* an expansive reaction which is the effect of indirect stimulation.

DIFFERENCE IN GEOTROPIC RESPONSE OF SHOOT AND ROOT

The next step is to endeavour to form some idea of the difference in the conditions of geotropic stimulation of the shoot and of the root, to account for the opposite responses in the two organs. The reason for this difference lies in the fact that in the shoot the perceptive and responding regions are one and the same; every piece of growing stem exhibits the characteristic geotropic curvature. In the root the case is different, since the perceptive and the responding regions are separated from each other. When the perceptive root-tip is removed the geotropic movement is either reduced or abolished. It must be borne in mind that this holds good

only in regard to gravitational stimulation, the seat of which is at the root-tip; for the decapitated root continues to respond to other forms of stimulation, such as chemical or photic.

Difference between Effects of Geotropic and Photic Stimulation

In the case of light, the source of stimulation is outside the plant; but in geotropism the force of gravity is by itself inoperative; it is only, as already explained, through the weight of the starch-grains contained in the geo-perceptive cells that the gravitational stimulus becomes effective. Want of recognition of this fundamental difference has led many observers to attempt to establish an identity of reaction of the root to geotropic and to photic stimulation, in spite of facts which plainly contradict it. The impulse under geotropic stimulation is originated at the root-tip, and transmitted to the growing region at a distance. This indirect stimulation makes the root *curve away* from the incident vertical lines of force of gravity. There is, however, no necessary restriction in regard to the point of application of light, which can be directly applied at the growing region, causing movement of the root *towards* the incident light.

The distribution of the cells (statocysts) containing the starch-grains in the shoot and in the root, furnishes material for an explanation of the different geotropic response of the two organs. In this connection the results of the investigations of Haberlandt and of Němec are highly suggestive. Haberlandt finds statocysts present in the responding region of the stem; in fact, every section of the growing stem not only possesses the responding tissue, but also the apparatus for initiating excitation—namely, the statocysts. The geotropic stimulation of the stem is therefore direct. Němec's investigations on the distribution of statocysts in the root show, on the other hand, that it is in the central portion of the root-cap that the cells

containing the starch-grains are situated; and this would account for the necessarily indirect geotropic stimulation of the growing region of the root.

The anatomical fact that the perceptive region in the root is separate from the responding region, explains the physiological difference between the two organs. Through whatever means the stimulus of gravity may act, it is inevitable, inasmuch as the stimulation of the shoot is direct and that of the root indirect, that an identical stimulation should induce responsive reactions of opposite sign in the two cases.

It will thus be seen that the postulation of two different irritabilities in the shoot and in the root is wholly unnecessary and unwarranted by facts. Experiment has shown that the irritability of the root is in no way different from that of other organs.

Summary

When the tip of the root is subjected to the stimulus of gravity, the upper half exhibits an excitatory reaction of galvanometric negativity indicative of direct stimulation.

The consequent electric response in the growing region above the stimulated root-tip is positive, indicative of increase of turgor and expansion. This is the effect of an impulse transmitted from the stimulated tip. The stimulus of gravity is perceived at the root-tip, whilst the responsive movement takes place in the distant growing region.

In contrast with the root, the growing region of the shoot both perceives and responds to geotropic stimulation.

As the effects of direct and indirect stimulation on growth are antithetic, the geotropic responses of shoot and of root cannot but be of opposite signs, since the stimulation is direct in the one case and indirect in the other.

There is no necessity for postulating different irritabilities for the shoot and the root, since it has been demonstrated that positive or negative curvature is dependent upon whether the stimulation is direct or indirect.

CHAPTER XXXIV

THE MECHANISM OF THE TWINING STEM

An unsupported twining stem bends over and its apex circumnutates in a path more or less circular. When in the course of circumnutation it comes across a support, it twines round it. The direction of movement is in a large number of cases against the hands of the clock, which I will distinguish by a plus sign; in a few cases it is negative or clockwise. It is, however, often difficult to say what the sign of normal movement actually is; for the same plant is found sometimes to move in an anti-clockwise and at other times in a clockwise direction.

No satisfactory explanation has yet been given of these movements. To quote Pfeffer: 'The factors which determine the permanent homodromous curvature of the apex are uncertain. . . The homodromous curvature of the apex is probably due to autonomic variations of tone, in which the external world and the progress of twining act as directive stimuli. Baranetzky and Noll on insufficient grounds assume the existence of a dia-geotropic irritability in the apex inducing paranasty. Ambronn ascribes the homodromous curvature to the conjoint action of circumnutation and negative geotropism, a conclusion which Schwendener disputes. The latter erroneously regards circumnutation and geotropism as factors of constant magnitude, and forgets that the circumnutation and the klinotropic position of the shoot caused by it are themselves the result of regulated geotropic reactions. De Vries supposed the curvature to be due to the torsion produced by

the weight of the free portion of the apex, but this has been shown to be untrue by various investigators. The causes of twining are therefore unknown.'[1] There has been much discussion in regard to the question whether circumnutation is autonomous or whether it results from the action of some external stimulus.

Characteristic Response of Anisotropic Organs

The torsion, or twisting growth, characteristic of the twining stem is the result of the unequal growth of two opposite sides. The stem is, in fact, anisotropic; it may be regarded as consisting, at any given moment, of two diverse longitudinal halves, which differ not only in their rate of growth but also in their degree of excitability so that they are differently affected by an identical change in the environment. The differentially growing stem may be compared with the anisotropic pulvinus of Mimosa. The upper and the lower halves of the pulvinus are excitable, but in a different degree. Local stimulation of the upper half produces a contraction of that half, causing an up-movement, while local stimulation of the lower causes a more vigorous down-movement. Diffuse stimulation causes antagonistic reactions in the two halves, but since the contraction of the lower half is greater, the predominant effect is a resultant down-movement. For the sake of simplicity the antagonistic action of the upper half may be ignored, and the responsive movement attributed mainly to the action of the more active half of the organ. The essential difference between the anisotropic pulvinus of Mimosa and the anisotropic stem of twining plants is that the plane which demarcates the two diverse halves in the former is fixed; whereas in the latter it regularly travels from segment to segment of the circumference in a slow revolving motion.

Whilst the action of the less active half of a twisting organ may, in general, be ignored, some complications may

[1] Pfeffer, ibid. vol. iii. p. 3[illegible].

arise from the fact that the optimum point of some variation such as a change of turgor or a change of temperature, may be reached earlier in the more active half than in the less active.

Preliminary Adjustments

In working with cut specimens it is found that the torsion is at first clockwise (negative), instead of being anti-clockwise (positive). I was able to trace this reversal to the effect of the strong stimulation caused by section. If, after mounting, the cut specimen be left undisturbed, the normal torsion will be found to be fully restored after a period of rest of about an hour. In obstinate cases, recovery is hastened by immersion of the cut stem in tepid water. It should be borne in mind that any rough handling acts as a stimulus, and may thus retard or even reverse the direction of the normal torsion.

Autonomous Torsional Circumnutation

Experimental investigations have been carried out with a number of species of twining plants, such as *Thunbergia gigantea*, *Thunbergia coccinea*, *Porana paniculata*, *Ipomoea*, *Clitoria Ternatea*, and the common Phaseolus. The researches were carried out under widely varied climatic conditions. Tropical conditions prevailed in my Institute in Calcutta, the mean temperature for 24 hours being about 30° C. in summer. Colder conditions existed at my Research Station at Mayapuri, Darjeeling, situated at a height of 7000 feet, the mean temperature in summer being 18° C.

Experiment 201. *Rate of circumnutation.*—I will first describe the movement of the horizontally inclined apex of *Thunbergia coccinea* growing wild on the hill-side at Darjeeling. This movement of circumnutation is to be distinguished from the torsional movement of the erect stem. The method of observation of circumnutation will be understood from

fig. 214. The successive positions of the tip of the circumnutating plant are read at different hours of the day against a circular scale placed below, in order to determine the changing rates of movement due to external variations of intensity of light and of temperature. The rates during the hours of the day are given in the table.

TABLE XXXVIII.—RATES OF CIRCUMNUTATION DURING DIFFERENT HOURS OF THE DAY (*Thunbergia coccinea*).

Hours of the day	Rotation	Difference	Hours of the day	Rotation	Difference
5 A.M.	0°	...	2 P.M.	405°	15°
6 ,,	15°	15°	3 ,,	315°	−90°
7 ,,	37°	22°	4 ,,	340°	25°
8 ,,	130°	93°	5 ,,	380°	40°
9 ,,	230°	100°	6 ,,	400°	20°
10 ,,	280°	50°	7 ,,	412°	12°
11 ,,	325°	45°	8 ,,	424°	12°
12 Noon	370°	45°	9 ,,	435°	11°
1 P.M.	390°	20°			

As regards external conditions, the plant was in the shadow of surrounding trees up to 9 A.M., when sunlight fell on it directly and continuously till 3 P.M.; after this the rays of the sun were obstructed by trees on the other side. The temperature rose from 12° C. at 5 A.M. to the maximum of 20° C. at 2 P.M. Very strong sunlight and high temperature at 2 P.M. brought about a condition of drought which caused a reversal from anti-clockwise to clockwise movement. The incidental effect of drought will be described later in detail. The rise of temperature in the morning enhanced the rate of circumnutation up to 9 A.M., but sunlight caused increasing retardation; the effect of drought referred to above caused a reversal of movement after 2 P.M. As the sun disappeared behind the trees there was a recovery to 25° between 3 and 4 P.M. This increased to 40° between 4 and 5 P.M. After 5 P.M. the temperature fell rapidly, causing diminution in the rate of movement. The above example shows in a general way how the conjoint effects of changes of intensity of light, of temperature,

and of condition of turgor modify the circumnutation of the twining shoot. The effect of these different factors on the movement of the shoot will be presently considered in greater detail.

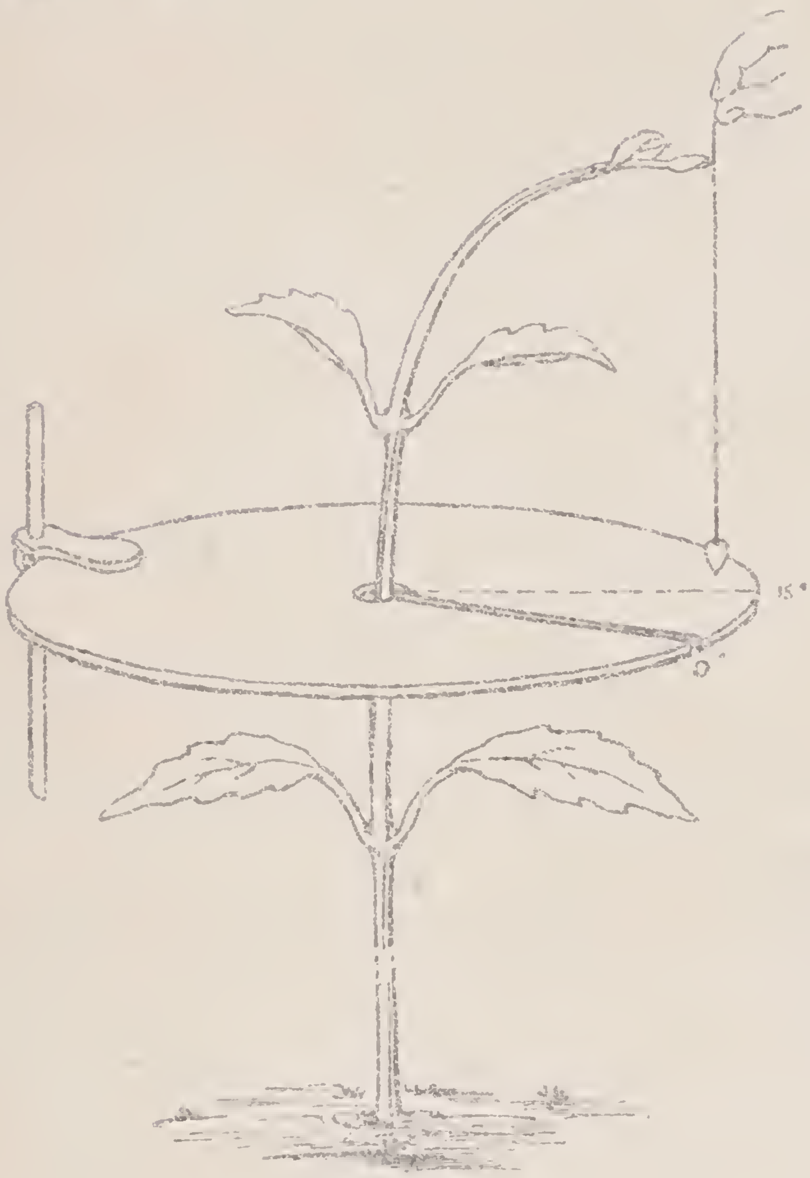


FIG. 214.

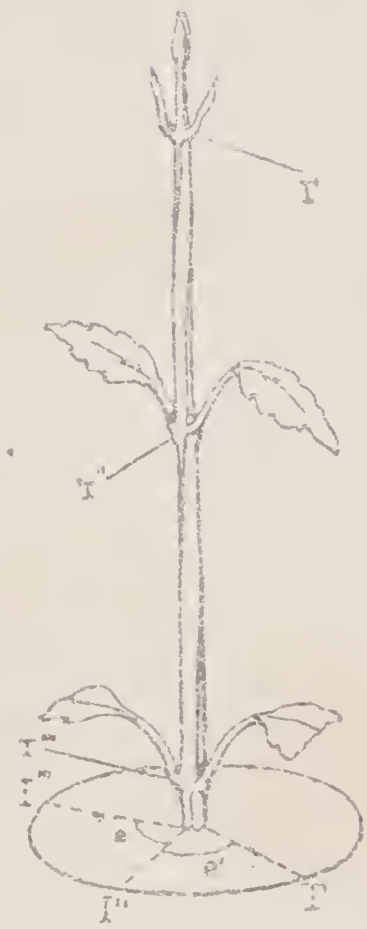


FIG. 215.

FIG. 214. Method of measurement of Circumnutation of a twining shoot.

FIG. 215. Measurement of relative activities of successive internodes. I', I'', I''', indices fixed at different nodes.

Experiment 202. *Torsional rotation round the vertical axis.*—The observation was continued the next day with the same plant with this difference, that the horizontally inclined portion of the stem was now held erect by means of a long and thin piece of string passing over a pulley, the end of the string being attached to a suitable counterpoise: the string itself was practically torsionless. A fibre of

glass was attached to the apex of the stem, to serve as an index. The object of holding the stem erect was to eliminate the action of lateral geotropism, so called. In spite of this, the erected stem exhibited a rotational movement similar to that of the stem when inclined.

TORSIONAL ACTIVITY OF DIFFERENT INTERNODES

Experiment 203.—For the determination of the relative activities of different internodes, suitable indices were attached to the plant at the corresponding nodes. The fixed circular scale serves for the measurement of the torsional rotation. The index at the tip of the stem indicates the total rotation. The difference between the angles described by I′ and I″ measures the torsional rotation of the first large internode. Similarly, the different activities of successive internodes from top to bottom may be measured (fig. 215). The results are given in Table XXXIX.

TABLE XXXIX.—RATES OF ROTATION OF SUCCESSIVE INTERNODES.

Different nodes	Rotation	Difference
Rotation of tip	55°	...
,, second internode . .	40°	15°
,, third internode . . .	8°	32°
,, fourth internode . .	3°	5°
,, fifth internode . . .	0°	3°

Taking the position of the lowest index, which did not move, as zero, the torsion of the first or highest internode is 15°. Torsion rises to a maximum of 32° at the second internode, where the rate of growth is also at its greatest. The rate declines to 5° at the third, and to 3° at the fourth. There is no rotation in the fifth internode, which was the oldest. Old internodes occasionally exhibit a slight rotational movement which is negative, *i.e.* opposite to that of the normal.

The results of the experiments just described prove that

the stems of twining plants have an autonomous torsional activity which is not dependent upon geotropism. This will be clear when it is realised that it is differential growth which causes the torsional movement, growth itself being a phenomenon of autonomous activity. The stimulus of gravity, it is true, modifies growth, but does not initiate it. Examination of the ribbed stem of a twining plant before it has bent over shows that the erect stem had undergone a twist (fig. 216). Circumnutation of the bending stem is thus principally due to the torsional activity of the organ. When the circumnutating stem encounters a more or less vertical support, it coils round it.

FIG. 216. The twist of the ridges of the stem (left figure) indicates the natural torsion of the stem. The right figure exhibits shoot twining round support in anti-clockwise direction (Thunbergia coccinea).

CONTACT-STIMULUS AND TWINING

Kohl found that the stem of Calystegia twined round a loose string, the stem being concave at all points of contact. In spite of this, there is a prevalent opinion that twining stems are not sensitive to the stimulus of mechanical contact, a view which raises difficulties in explaining the primary cause of twining round a support. In the case of tendrils which are highly sensitive to contact, twining is produced by the retardation of growth at the points of contact, aided by acceleration of growth of the

distal side (p. 97) I subjected the matter to the following experimental test.

Experiment 204.—My High Magnification Crescograph enabled me to obtain a record of the normal rate of growth of the stem of Thunbergia; this was found to be 0·7 μ per second. The stem was next subjected for 5 minutes to mechanical stimulation by friction applied to all sides of the organ. The growth was now found to be arrested, and it was not till after an hour that growth was renewed. It is evident that continuous stimulation of one side of the stem by friction against a rough support retards or arrests the growth, with induced concavity, of the stimulated side. The twining stem is therefore sensitive to mechanical stimulation.

The following may be taken as the sequence of events which lead to twining. The autonomous torsion of the stem gives rise to circumnutation of the overhanging part of it, in the course of which movement the stem comes in contact with a support. Continued autonomous torsion and the contact-sensitiveness of the stem then co-operate to effect the twining.

Having now indicated what is the essential mechanism of twining, I may proceed to explain several sensitive methods for the measurement of the torsional movement and its induced variations.

Method of Optical Magnification

In order to study the effect of the change of any one of the external factors, it is essential to maintain all other factors absolutely constant, a condition which can be secured only for a short time. Hence necessity arises for rapid observation of the rate of normal torsion, and of the changes induced in it by external agents. This I secured by the Optical Method which I devised for my earlier investigations on autonomous torsion ('Plant Response,' 1906). The tip of the plant is attached to a thin, torsionless string which passes over a pulley with a suitable counterweight at the other end; the plant is thus held erect. A light concave

mirror, fixed at the upper end of the stem, reflects a spot of light on to a scale which may be placed at a distance of 3 metres, the scale itself being divided into millimetres. The magnification thus produced is then 6000 times, which is sufficient to measure the rate of torsion in the course

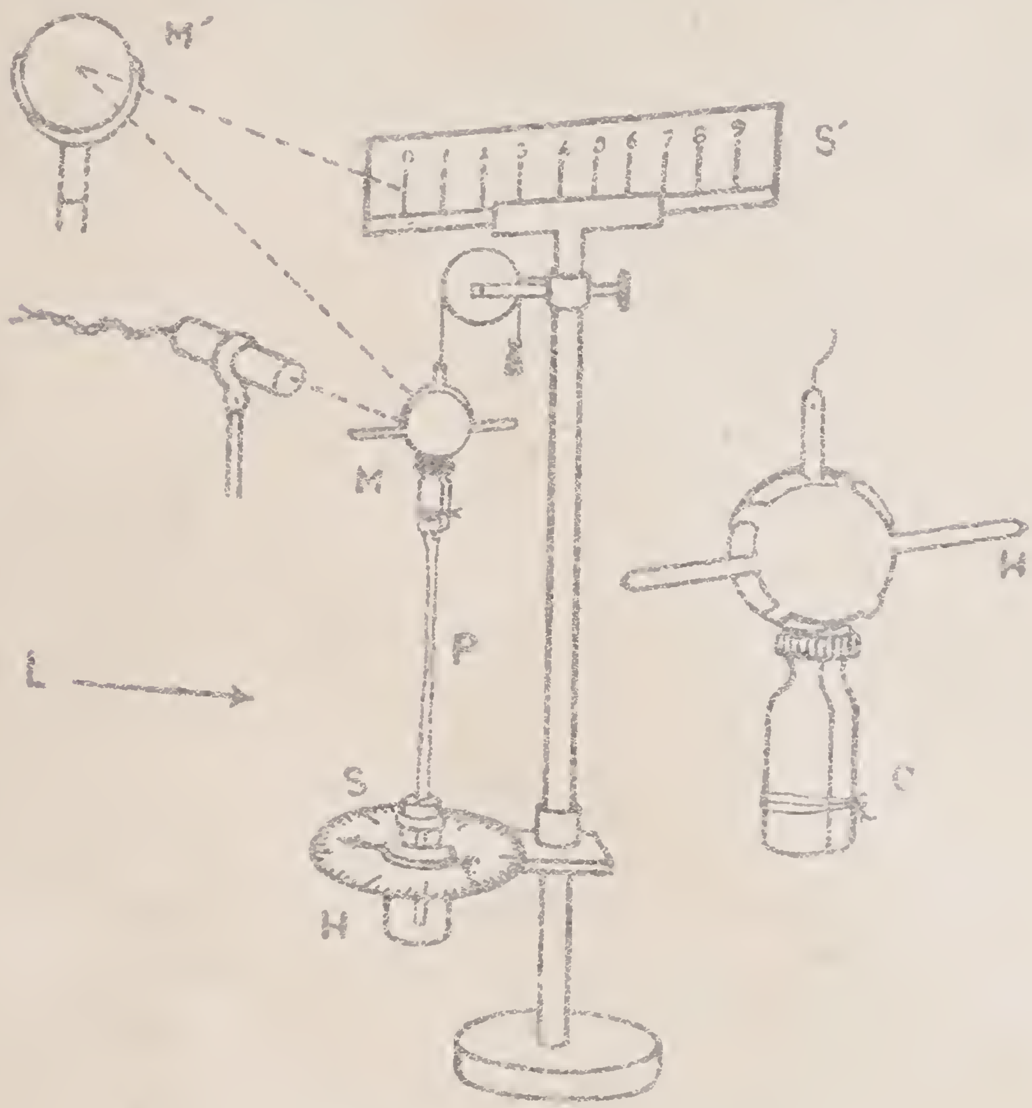


FIG. 217. Method of Optical Magnification

P, stem, upper end of which is held in clamp C (shown in the side figure); M, plant-mirror; M′, fixed mirror; S′, scale for measurement of torsion. Plant held at lower end in a small phial filled with water.

of a minute. Certain precautions have to be taken in attaching the string to the tip of the plant. The very crude method of tying a knot gives rise to unequal pressure on different sides of the organ, resulting in the transmission of unequal excitations down the stem. To avoid this, cotton-wool is wrapped round the tip, to act as a soft cushion. A light three-pronged aluminium clamp now holds the tip of the plant. A spring clip attaches the plant-mirror to the clamp (fig. 217).

I find that it is more convenient to work with a cut specimen than with an intact plant; the effect of wound disappears after a time, when the stem regains its normal torsional activity. The cut end of the stem is fixed by means of a cork in a small phial filled with water. This plant-holder H passes through a circular scale; by rotation of H, different flanks of the plant can be subjected to unilateral action of light L. The light from a pea-lamp is reflected from M and re-reflected on the millimetre scale S by means of a second stationary mirror M′ at a distance of 75 cm., the magnification produced being 3000 times. The rate of movement is observed every 5 minutes, the intervals being signalled by clockwork. It may be said in general that the rate of autonomous torsion depends on the species of the plant, on its physiological vigour, and on external condition, such as season and temperature.

Automatic Recorder

Method of Magnification.—I also succeeded in the difficult task of obtaining an automatic record of the normal rate of torsion and its induced variations. The method will be understood from the diagrammatic representation given in fig. 218. The clamp bears a light aluminium index I, about 10 cm. in length, which presses against V, a vertical projection from the short arm *l* of a lever, the vertical fulcrum-rod of which rests on a conical jewel-support *p*. The short arm is 0·5 cm., while the longer arm L is 15 cm. The total magnification of the system of levers is therefore about 300 times. By slightly tilting the apparatus, the recording end of L on the left tends to rest on the smoked-glass recording plate G. The vertical projection V at the other end of the lever then presses against the index I. This latter is pushed to the left by the anti-clockwise rotation of the shoot, while the recording end of L is moved towards the right. It must be remembered that the recording index is moving in a horizontal plane; hence, in order to obtain a dotted record, the recording

plate has to be moved up and down by means of clockwork. The recording plate has a movement from right to left, and an oscillating movement up and down, at intervals of 2 minutes. The slope of the dotted record shows the rate of natural torsion. An enhancement induced in the rate

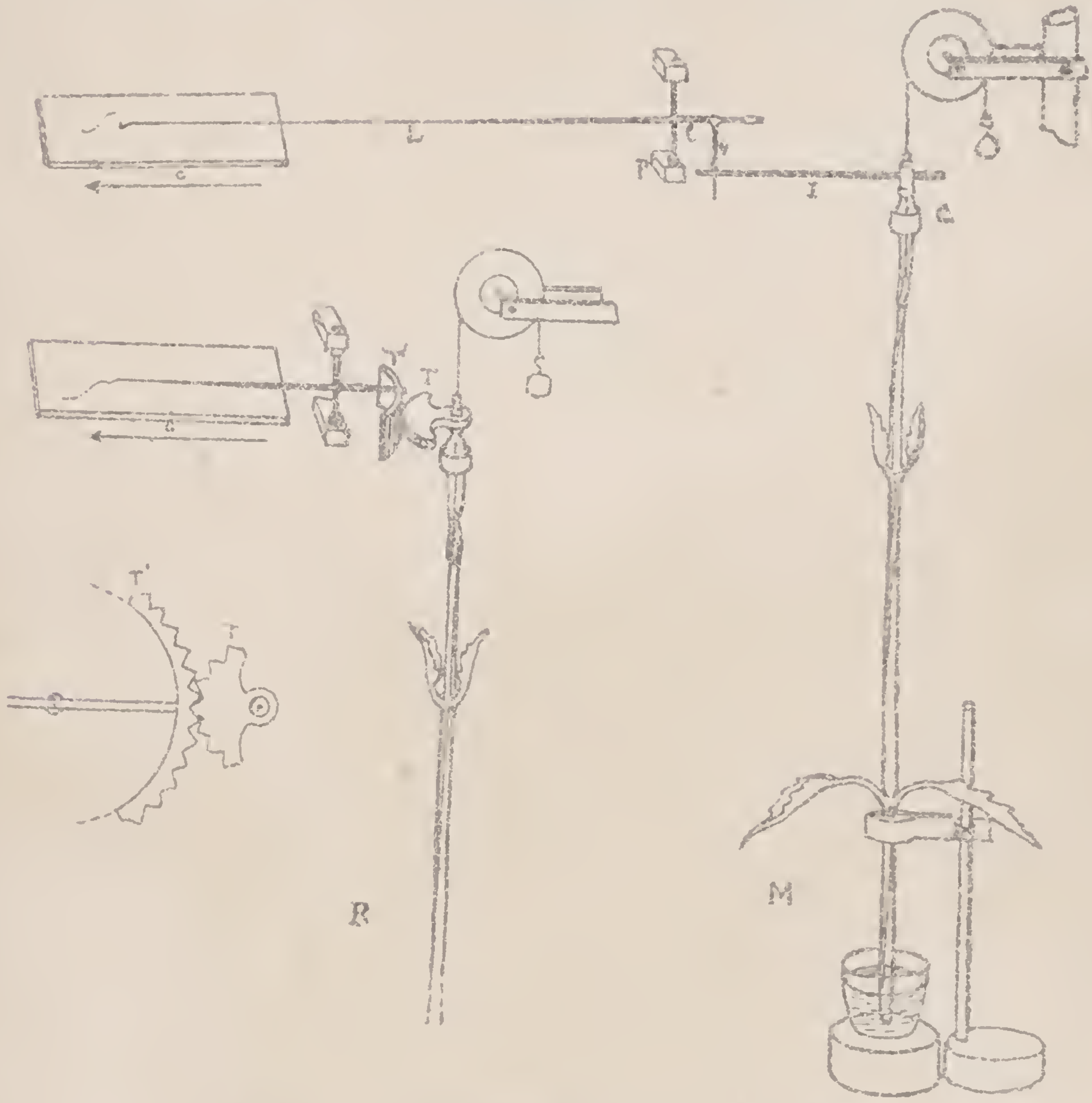


FIG. 218. Automatic Recorder of Torsion.
M, method of magnification; R, method of reduction. (See text.)

causes an erection of the curve, while a diminution causes a flattening. If the natural torsion becomes reversed, the index I moves in clockwise direction, and the record is correspondingly reversed from an ascending to a descending curve.

Method of reduction.—A continuous record for 24 hours was necessary for my investigation of the diurnal variation of torsional movement described in the next chapter. The total rotation during 24 hours was too great to be recorded

in the plate. The problem to be solved was therefore not one of magnification but of reduction. This was secured by the employment of a device which produced a suitable reduction by a system of aluminium toothed wheels T and T′ (fig. 218, R). The necessary condition for perfect working of the arrangement is that the centre of curvature of the toothed wheel T′ should be at the fulcrum of the recording lever.

Having explained the method of observation and of record of torsional movement, I describe in this chapter the results of the investigations of the following subjects:

1. Modification of torsional movement by variation in the rate of ascent of sap.
2. Torsional movement under variation of temperature.
3. The critical fatal temperature.
4. Effect of chemical agents on autonomous torsion.

Effect of Variation in the Rate of Ascent of Sap

I have shown[1] that the rate of ascent is increased, within limits, by a rise of temperature of the water applied at the cut end of the stem. Diminution of the rate of ascent is produced under drought or by withdrawal of water. Artificial drought may also be caused by the application of a plasmolytic solution of KNO_3 at the cut end of the stem. Increase in the rate of ascent causes an increase, while diminution in the rate gives rise to diminution of turgor in the stem. *The experiments show that an increase of turgor, however produced, causes an increase in the rate of normal torsion. Diminution of turgor, on the other hand, causes an arrest or even a reversal of normal torsion.*

Experiment 205.—The normal rate of the anti-clockwise torsion of the stem of Phaseolus was 10 mm. per 5 minutes. The vessel which supplied water at the cut end of the stem was removed; the effect of the resulting drought was a continuous diminution in the rate of the anti-clockwise

[1] *Physiology of the Ascent of Sap*, p. 98.

torsion. This culminated, in the course of half an hour, in an actual reversal to negative or clockwise torsion of − 25 mm. per 5 minutes.

I next studied the effect of application of warm water to the cut end of the stem. The resulting increased rate of ascent of sap converted the negative − 25 to positive 20, which is greater than the original rate. Water was withdrawn once again, and the torsion became reversed to − 5. Warm instead of tepid water was next applied at the cut end, with the result that the negative became replaced by an enhanced positive of 50. The above is typical of numerous experiments.

Experiment 206. *Effect of plasmolytic withdrawal of water.*—Artificial drought was produced by the application of a plasmolytic solution of KNO_3 at the cut end of the stem. The normal rate in a specimen of Phaseolus was + 14; application of KNO_3 solution at the cut end caused a reversal to − 6 in the course of half an hour.

The effect of variation in the rate of ascent of sap on torsional response will now be related with the effect induced in growth itself. I have already shown (p. 53) that normal growth is accelerated by enhancement of turgor caused by increased rate of ascent of sap, drought producing the opposite effect. The relation between changes in the rate of growth and of torsion will be seen by comparison of the two following tables:

TABLE XL.—EFFECT OF ALTERNATE VARIATION OF TURGOR ON LONGITUDINAL GROWTH (ZEPHYRANTHES).

Condition of experiment	Rate of growth
Dry soil .	0·04 μ per sec.
Application of warm water	0·20 μ ,,
Application of KNO_3 solution .	0·01 μ ,,

TABLE XLI.—EFFECT OF ALTERNATE VARIATION OF TURGOR ON TORSIONAL GROWTH (PHASEOLUS).

Condition of experiment	Rate of torsion per 5 minutes
Normal . .	10
Withdrawal of water	− 25
Tepid water . .	20
Withdrawal of water	− 5
Warm water . .	50
Normal .	14
KNO_3 solution .	− 6

Effect of Variation of Temperature

For studying the effect of variation of temperature, either fall or rise, it is necessary that the variation should be gradual and not abrupt: for sudden variation acts as a shock, causing excitatory reaction.

Method of gradual variation of temperature.—This is accomplished by enclosing the plant within a double-walled cylindrical chamber made of highly conducting copper. Warm or cold water from a reservoir enters the hollow cylinder, and leaves it by a pipe provided with a stop-cock. By careful manipulation of the stopcock it is possible to change the temperature of the enclosure very gradually, the rate of variation being approximately 1° C. per 1½ minutes.

Effect of lowering the temperature.—The following results were obtained with two different species of plants, Porana and Thunbergia.

Experiment 207.—With falling temperature, the normal rate gradually diminished in both till the torsional movement was practically arrested at or about 9° C. There was a revival of growth on raising the temperature above this critical point. My other investigations have shown that various physiological activities are also arrested at a critical temperature. For example, the photosynthetic activity of Hydrilla is arrested at 9·5° C.

Table XLII.—Effect of Lowering the Temperature (Porana paniculata)

Temperature, °C.	Rate of torsion in m.m. per minute
23	54
20	31
18	22
15·5	18
1[illegible]	10
9	0

Table XLIII.—Effect of Cyclic Variation of Temperature (Thunbergia).

Temperature, °C.	Rate of torsion (through descent)	Rate of torsion (through ascent)
20	21	[illegible]
17	12·5	12
15	10	9·5
12	8	7·5
9	2	2

Table XLII gives the diminution of the rate of torsional movement in Porana by falling temperature. Table XLIII

gives the changes induced in Thunbergia by a cyclic variation of temperature, first of thermometric fall to the critical point, and then of rise to normal temperature.

Effect of rise of temperature.—The torsional activity increased with rise of temperature till an optimum was reached. Two different types of effect were observed, as described below.

Experiment 208.—The first type is exemplified by Porana. The activity increased till the optimum temperature was reached, which is between 32° and 33° C.; above this point it underwent a decline. It may be stated here that my other investigations show that the optimum temperature for growth, for photosynthesis, for ascent of sap, for transpiration, and for maximum sensibility of Mimosa, is also about 33° C. This characteristic, it should be remembered, relates to plants in the tropics.

TABLE XLIV.—SHOWING VARIATION OF TORSIONAL ACTIVITY UNDER RISE OF TEMPERATURE (PORANA)

Temperature. °C.	Rate of torsion per minute
23	14
26	24
31	52
32	54
35	28
38	18
42	10
43	5

Experiment 209.—Thunbergia represents the second type in which there are two optima instead of one. The rate of torsion increased up to 32° C., which is the first optimum. There was then a continuous decline till 40° C., after which the rate showed a sudden increase, reaching its maximum at 47° C., which is the second optimum. This double optimum will be noted in the record given in fig. 210, where the violent contraction at 60° C. is the death-spasm which will now be explained.

THE CRITICAL FATAL TEMPERATURE

As the temperature is raised above the optimum, a very abrupt and striking change occurs at a critical temperature of about 60° C.

FIG. 210. Death-spasm at fatal temperature of 60°. Note double optima before reversal. (Thunbergia.)

Experiment 210.—The results are graphically represented in the automatic record obtained with Thunbergia, during rise of temperature between 23° and 60° C. (fig. 219). It will be seen that the rate of torsion continuously increased till a diminution of the rate occurred above the first optimum at 32°; with further rise of temperature to about 40°, a second optimum was attained. At

60° C., however, a spasmodic *reversal* of torsional movement occurred, which was so violent that the record went down off the plate in a very short time.

Explanation.—I have shown that an erectile movement is produced in the leaf of Mimosa, under rising temperature, by the expansion of the more excitable lower half of the pulvinus. But a sudden spasmodic fall takes place at the critical temperature of 60° C., which is the spasm of death. This critical temperature is more or less definite in fresh and vigorous specimens. Growing organs likewise exhibit a sudden contraction at the fatal temperature (p. 37). It may fairly be inferred that the sudden reversal of normal torsion at this critical temperature is due to the violent death-contraction of the more active longitudinal half of the stem.

ACTION OF CHEMICAL AGENTS ON TORSION

A chemical solution applied to the cut end of the stem ascends with the rising sap and affects the torsional

FIG. 226. Effect of Formaldehyde applied at arrow, showing preliminary acceleration followed by reversal. A preliminary portion of the record is omitted. Successive dots at intervals of 3 minutes.

activity. A certain interval necessarily elapses between the application and the responsive reaction. In an experiment

with gas or vapour they are blown into the cylindrical chamber surrounding the plant.

Experiment 211. *Formaldehyde.*—The typical action of poison is exemplified by the effect of the application of 7 per cent. solution of formaldehyde to the cut end of the

FIG. 221. Effects of Chloroform and Ether on autonomous torsion

The record to left shows the effect of chloroform applied at arrow. There is a preliminary acceleration followed by reversal.

The record to right shows marked acceleration under dilute vapour of ether.

stem. My investigations on the effect of poison on growth has shown that the preliminary effect is an enhancement of growth, followed by arrest and by the death of the plant, often signalised by a spasmodic contraction (p. 46). In the case of the twisting growing stem, the automatic record (fig. 220) shows the different phases of reaction. The immediate effect of poison is an enhancement of the rate of normal torsion, seen in the wider spacing of the successive dots. This

continued for 12 minutes, after which the rate of movement diminished and became arrested after a further period of 24 minutes; the response now became reversed from positive to negative; all responsive movement disappeared in the course of an hour after application of the toxic agent, indicating complete poisoning of the stem.

Ammonia vapour abolishes the torsional activity. The vapour of hydrochloric acid is also toxic, producing an arrest of movement.

Experiment 212. *Chloroform.*—I give in the record to the left (fig. 221) the effect of chloroform vapour. It is seen to produce a preliminary enhancement of the rate, followed by reversal and arrest in the course of half an hour.

Experiment 213. *Ether.*—Ether is less toxic and its effect in a moderate dose is an enhancement of the rate of torsion which persists for a considerable length of time (record to right, fig. 221). Very prolonged application, however, induces depression in the rate.

SUMMARY

The growing twisting stem is anisotropic, two longitudinal halves at any given moment being unequally excitable, like the two halves of the pulvinus of Mimosa. The plane of demarcation between the two halves in Mimosa is fixed; in the twisting stem the plane slowly travels round the axis.

The torsion of the stem is autonomous: it is the result of the unequal growth of the diverse longitudinal halves.

The twining of the stem is effected by its autonomous torsional growth and by its sensitiveness to contact.

By the Method of Optical Magnification the rate of torsional growth can be accurately observed. The Automatic Method records the actual rate of torsional movement.

The rate of torsional growth is modified by the rate of ascent of sap. Enhancement of the rate of ascent induces

an increase in the rate of torsion; while depression of ascent, as well as plasmolytic withdrawal of water, induces retardation of the rate or reversal of the direction of torsion.

Rise of temperature up to an optimum induces an enhancement of the rate of torsion; lowering of temperature brings about a depression of the rate, or an arrest of the movement.

At the critical temperature of about 60° C. there is a reversal of the direction of torsion, which is the spasm of death.

A feeble dose of chloroform enhances the rate, but a strong dose causes arrest or reversal.

Ether in moderate dose greatly enhances the rate of torsional growth.

CHAPTER XXXV

EFFECT OF DIFFUSE STIMULATION ON AUTONOMOUS TORSION

THE effects of different modes of diffuse stimulation on autonomous torsion will be specially studied in this chapter. I begin with the effect of electric stimulation.

RESPONSE TO ELECTRIC STIMULATION

The great advantage of the electric mode of stimulation is that (1) it causes no mechanical disturbance in the record, and that (2) the intensity can be increased from minimal to maximal by the gradual approach of the secondary to the primary coil. The two electrodes from the secondary coil are applied one above and the other lower down on the stem, so that the induction current passes along the length of the organ. Since the effect of stimulus is additive, the effectiveness of stimulation depends on the product of intensity and duration. A minimal stimulus may thus become maximal by prolonging the duration of application.

As in other responding organs, a certain period elapses between the reception of stimulus, and the response, which continues for a time even after the cessation of stimulation.

EFFECT OF STRONG STIMULATION

Experiment 214.—I will first describe the effect of electric stimulation applied for 2 minutes on a vigorous specimen of Thunbergia. The normal rate was 28 mm. per minute. In response to stimulation the normal rate in the positive direction was diminished, culminating in reversal of direction to negative 3 minutes after the application

of stimulus. The negative attained its maximum of − 55 after a further period of 5 minutes. The specimen then exhibited recovery, which was completed in the course of about an hour. The results are given in the following tabular form :

TABLE XLV.—EFFECT OF MAXIMAL STIMULUS ON TORSIONAL RESPONSE OF VIGOROUS THUNBERGIA

Effect of stimulation	Rate of torsion per minute	Effect of stimulation	Rate of torsion per minute
Normal	28	After 6th min	− 30
After 1st min	25	,, 7th ,,	− 50
,, 2nd ,,	10	,, 8th ,,	− 55
,, 3rd ,,	− 5	,, 9th ,,	− 32
,, 4th ,,	− 7	,, 10th ,,	− 17
,, 5th ,,	− 15	,, 53rd ,,	25

I give the record of another experiment (fig. 222), in which the up-curve represents the normal torsion, the

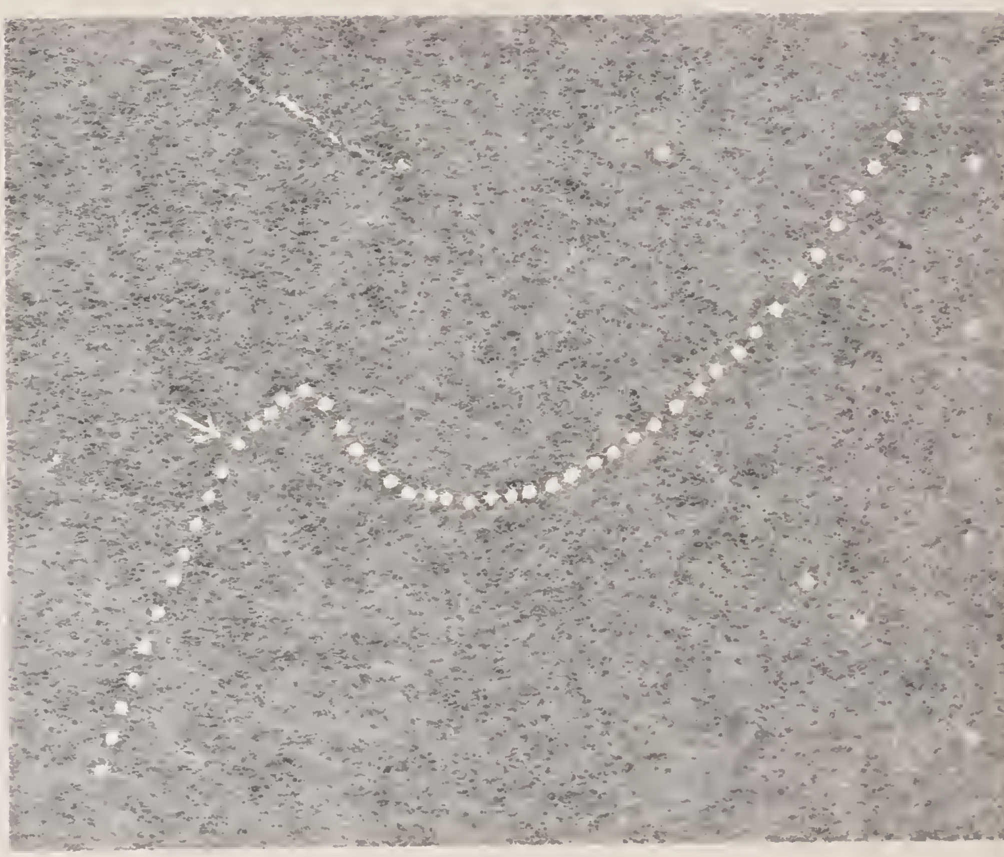


FIG. 222. Direction of torsion reversed under electric stimulation applied at arrow. Note gradual recovery. (Thunbergia.)

negative being represented by the down-curve. A reversal from positive to negative torsion after stimulation will be noticed, after which the response exhibited recovery.

The following table gives typical results obtained with different plants :

TABLE XLVI.—EFFECT OF STRONG ELECTRIC STIMULATION ON TORSIONAL RESPONSE.

Specimen	Normal rate per minute	After electric stimulation
Convolvulus . . .	25	− 4
Thunbergia . . .	12	− 20
,, . . .	25	− 2
Porana . . .	10	− 25

The results given in previous chapters have established the generalisation that all forms of maximal stimulation—electric, mechanical, or photic—induce a retardation of the rate of growth; that under increasing intensity or duration of the stimulus the retardation culminates in an actual contraction (p. 67). On this principle, it is retardation of the rate of growth and contraction of the more active half of the differentially growing stem that cause the diminution in the rate of torsion, culminating in actual reversal of direction, which follows strong stimulation.

EFFECT OF MINIMAL STIMULATION

In investigations on growth, I found that while a strong stimulus induces retardation, a feeble stimulus causes enhancement of the rate of growth. In the range of stimulation between minimal and maximal there is a critical intensity, above which there is retardation, and below which there is acceleration. The critical point is modified by the tonic condition of the organ, being relatively high in a subtonic specimen. It is therefore easier to obtain the enhancement of the rate of growth under stimulation in subtonic specimens. I found, moreover, that in such specimens the tonicity is improved by the stimulation, as manifested by a permanent increase in the rate of growth. In torsional response the rate of normal movement

may therefore be expected to be enhanced under the action of feeble stimulation.

Experiment 215.—A specimen of Thunbergia was in a slightly sub-tonic condition, as evidenced by its slow rate of torsion, which was 3 mm. per minute. The effect of *minimal stimulation* for 4 minutes is given in the following table:

TABLE XLVII.—EFFECT OF MINIMAL ELECTRIC STIMULUS IN ENHANCING THE RATE OF TORSION.

Effect of stimulation	Rate of torsion per minute	Effect of stimulation	Rate of torsion per minute
Normal	3	After 5th min.	43
After 1st min.	14	,, 6th ,,	42
,, 2nd ,,	19	,, 7th ,,	38
,, 3rd ,,	32	,, 25th ,,	5
,, 4th ,,	30		

The results show that feeble stimulation enhanced the rate from 3 to the maximum positive of 43 in the course of 6 minutes, after which there was the commencement of recovery. The improvement of the tonic condition is shown by the permanent enhancement of the rate from the original 3 to 5.

Other examples are given in the following table, in which the maximum enhancement and permanent after-effect are given in different columns.

TABLE XLVIII.—EFFECT OF MINIMAL STIMULATION IN ENHANCING THE RATE OF TORSION IN DIFFERENT PLANTS.

Specimen	Normal rate per minute	Maximum acceleration	After-effect
Porana	6	22	8
Thunbergia . . .	4	26	8
Convolvulus . . .	7	20	10

It has been stated that the effect of stimulation is cumulative. Hence, with a stimulus of moderate intensity, the effective stimulation is minimal at the onset and only

becomes maximal after a certain duration of application. This explains the most frequently observed effect of stimulation—namely, a preliminary increase followed by a diminution in the rate of torsion.

Effect of Indirect Stimulation

Another important result which I have obtained is the effect of indirect stimulation on growth. Stimulation is said to be indirect when it is applied at some distance from the responding growing region. I have been able to establish the generalisation (p. 131) that while direct stimulation induces retardation, indirect stimulation causes enhancement, of the rate of growth.

The effect of indirect stimulation on autonomous torsion proves to be an increase in the rate of movement. Stimulation was effected indirectly by application of electric shock for 4 minutes to the cut stem below the clamp which supported it.

Experiment 216.—The specimen employed was Thunbergia, the normal rate being 8. As the result of indirect stimulation, the rate was increased to a maximum of 95 in the course of 6 minutes. The rate was restored to nearly the normal in the course of 40 minutes. Other examples are given in the following table:

TABLE XLIX.—EFFECT OF INDIRECT STIMULATION IN ENHANCING THE RATE OF TORSION.

Specimen	Normal rate per minute	Maximum increase
Porana	10	36
"	7	42
Thunbergia . . .	10	37

Effect of Thermal Shock

It may be said in general that any sudden variation of external conditions constitutes a stimulus. Electric stimulation by an induction current is due to abrupt change of

the electric potential. I have found that a sudden variation of temperature also acts as a stimulus.

Experiment 217.—I have already explained that a steady rise of temperature up to an optimum enhances the rate of torsion. In the present experiment a specimen of Clitoria was mounted within a double cylinder through which a flow of water at the constant temperature of 25° C. was maintained. The rate of normal anti-clockwise movement was 12. Warmer water at 30° C. was now made to flow through the cylinder, thus subjecting the plant to a sudden variation of temperature. The result was an abrupt reversal in the torsional movement from 12 to − 75. This persisted for 2 minutes. As the temperature became steady, the movement was gradually converted from negative to positive. After half an hour it had become 14, slightly greater than at the beginning. This is due to the fact that the steady temperature inside the cylinder was now about 28° C.

Effect of Mechanical Stimulation

Experiment 218. *Feeble stimulation.*—The normal rate of Thunbergia was 20, which was increased to 40 under the application of a feeble mechanical stimulus. The recovery to the normal rate of 20 was attained in 5 minutes.

Experiment 219. *Effect of stronger stimulation.*—Stimulus of friction was applied by rubbing the specimen lengthwise with a piece of fine emery paper for about 3 minutes. The normal rate in Porana was 55; after the frictional stimulation the rate was diminished to 3. The specimen exhibited a recovery of the normal rate in the course of 20 minutes.

It has been shown (Experiment 50) that frictional stimulation induces a general retardation of growth. In a twisting stem the retardation is the greater in the more actively growing half, which is also the more excitable. This differential effect causes a diminution of the rate, or even a reversal of the direction, of normal torsion.

Experiment 220.—The next experiment was undertaken with Thunbergia, and stronger and more prolonged friction was applied. The normal rate was 38, which became reversed into − 22 after stimulation. The recovery was nearly complete in the course of an hour.

Effect of Direct and Indirect Stimulation by Light

With regard to the unilateral action of light, Pfeffer summarises the results as follows: 'According to Mohl, Dutrochet, Darwin, and Baranetzky, the circumnutating shoots of climbers are positively heliotropic, but this irritability is so weak as merely to somewhat accelerate circumnutation when the stimulus is applied so as to aid the autonomic movement, and slightly to retard the latter when acting against it.'[1] The relation to light is, however, more complex than has been supposed. I will first describe the effect of diffuse light acting on all sides of a twisting stem. Two mirrors, suitably inclined, were placed behind the stem, so that the incident sunlight acted on all sides of it. The plants had been previously kept in darkness for a short while.

Experiment 221. *Effect of diffuse sunlight.*—I describe experiments with two different plants—Porana and Thunbergia. The former was highly excitable, and the latter slightly subtonic; Porana was subjected to the stimulus of light for 5 minutes, and Thunbergia for 4 minutes.

The normal rate of Porana was 41; it exhibited an immediate diminution, which reached a minimum of 4, 8 minutes after the cessation of exposure to light. The recovery was practically complete after 50 minutes.

In Thunbergia the normal rate was 34; the rate exhibited a preliminary enhancement which persisted till the fourth minute, after which retardation set in, the maximum retardation being at the tenth minute when the rate was reduced to 2. After this there was slow recovery,

[1] Pfeffer, *ibid.* p. 41

and the rate was 24 at the twenty-fifth minute. The results are given in detail in the following tabular statements.

TABLE I.—EFFECT OF DIFFUSE SUNLIGHT ON PORANA.

Effect of stimulation	Rate of torsion per minute
Normal	41
After 1st minute	34
,, 2nd ,,	24
,, 3rd ,,	12
,, 4th ,,	10
,, 5th ,,	8
,, 6th ,,	7
,, 7th ,,	6
,, 8th ,,	4
,, 50th ,,	39

TABLE II.—EFFECT OF DIFFUSE SUNLIGHT ON THUNBERGIA.

Effect of stimulation	Rate of torsion per minute
Normal	34
After 1st minute	42
,, 2nd ,,	40
,, 3rd ,,	30
,, 4th ,,	28
,, 5th ,,	[illegible]
,, 6th ,,	18
,, 7th ,,	12
,, 8th ,,	2
,, 25th ,,	24

The results given above show that the effect of the stimulus of light is the same as that of other modes of stimulation. The effect of minimal stimulation is seen in the preliminary enhancement of the rate of torsion, while maximal stimulation caused a retardation of the rate. When exposure to light is continued for a longer period, the retardation culminates in actual reversal.

Effect of red and of blue light.—In my investigation of growth under the action of light of different colours, I found that blue light was very effective in the retardation of growth. Red light induced practically no retardation (p. 78). I could not be quite certain if it did not induce the opposite effect of enhancement.

The contrasted effects of red and of blue light on autonomous torsion are, however, very marked. The different lights were obtained by means of colour-filters placed in the path of strong white light.

Experiment 222.—The normal rate of torsion in Thunbergia was 14; this was enhanced to 38 under continuous exposure to diffuse red light. On the cessation of light there was a complete recovery to the normal rate of 14 in the course of 15 minutes. The same specimen was next subjected to the action of blue light. The retardation was

immediate and the rate was reduced from 14 to 3 in the course of 8 minutes. On the cessation of exposure to light, recovery was found to be complete after an interval of half an hour. A second specimen gave very similar results.

Experiment 223. *Effect of indirect stimulation by light.*—In Thunbergia the normal rate of 20 was enhanced to 60 by indirect stimulation by light applied for 1 minute. The recovery was complete in the course of half an hour. In Porana, similarly, indirect stimulation by light enhanced the rate from 8 to 38. The effect of indirect stimulation by light is similar to that of indirect electric stimulation.

Effect of Geotropic Stimulation

In order to obtain a satisfactory explanation of the effect of geotropic stimulation on autonomous torsion, it is necessary to obtain a clear idea of the means by which that stimulation is effected. The experiments that have been described in previous chapters fully confirm the theory that it is the statolithic particles in the statocysts which cause geotropic stimulation (*see* p. 342).

I have already shown that the apical ends of the statocysts are more sensitive than the basal ends (p. 356). In that case, a maximum variation in the geotropic action should occur in two positions, erect and inverted—*i.e.* at inclinations of 0° and 180°. The question now arises whether this would be confirmed by observations made on an organ performing torsional growth.

Since in such organs the effect of more intense stimulation is manifested by a greater retardation of the rate of torsion (which may culminate in reversal), it is quite possible to observe the effect of geotropic stimulation in the two positions, erect and inverted.

Experiment 224.—The mode of procedure is as follows: The rate of torsion is observed by the optical method, first when the stem is erect, and afterwards when it is upside down. It is to be understood that the observer is looking at the rotating apex of the stem from above in the erect,

and at the base in the inverted, position. The tabulated results show that in the inverted position the rate of rotation invariably underwent a marked diminution, the statolithic particles now press against the apical ends of the cells, which are thus shown to be the more excitable.

TABLE LII.—EFFECT OF GEOTROPISM IN INVERTED POSITION IN RETARDATION OF TORSION.

Specimen	Normal rate per minute	Rate in inverted position
1. *Momordica monadelpha* .	21·5	[illegible]·5
2. *Clitoria Ternatea* . .	8·[illegible]	2·5
3. *Vitis quadrangularis* . .	5·5	0·8
4. Phaseolus	6·0	3·0

Experiment 225. *Reversal of torsion.*—In highly sensitive specimens, inversion of the plant did not merely retard the rate of torsion, but induced an actual reversal of its direction. Thus, in a specimen of Porana the rate in the erect position was 23. When inverted, the torsional movement was found to have undergone an actual reversal to negative—that is to say, the direction of torsion was now with the hands of the clock, at a rate of − 5.

In the next series of experiments, observations were taken with specimens erect, then inverted, then erect again, in order to eliminate the effect of any chance variation. These repetitions induce fatigue, so that the response on re-erection of the stem is sometimes less than at the beginning. In vigorous specimens, however, there is but little decline. The following table gives results obtained with a number of different plants:

TABLE LIII.—GEOTROPIC REACTION IN DIFFERENT POSITIONS—ERECT, INVERTED, AND RE-ERECTED.

Specimen	Erect position	Inverted position	Re-erected position
Thunbergia .	14	− [illegible]	[illegible]
„ . . .	35	− [illegible]	[illegible]
Porana . . .	1[illegible]	− [illegible]	[illegible]

Summary

Direct electric stimulation of adequate intensity induces a retardation of torsional response which may culminate in actual reversal.

Minimal electric stimulation, as well as moderate stimulation of a subtonic specimen, induces enhancement of the rate of torsion.

Indirect stimulation causes an acceleration of the rate of torsion.

Sudden thermal variation acts as a stimulus and causes retardation or even a reversal of direction of torsion.

Mechanical stimulation induces retardation or reversal of torsion according to the intensity of stimulation.

Under diffuse stimulation by strong light the rate of torsion undergoes diminution.

Red light induces an enhancement of the rate of torsion, while blue light induces a marked retardation.

Geotropic stimulation has a definite influence on the rate of normal torsion. When the stem is held inverted, the rate of normal torsion undergoes a retardation which may even culminate in an actual reversal of the direction of torsion, proving that geotropic stimulation is more effective in the inverted position. Facts have already been adduced which show that the excitability of the ectoplasmic layer at the apical end of the geo-perceptive cells is greater than at the basal end. In the inverted position the heavy particles, which are supposed to cause geotropic excitation, press against the apical ends. The retardation of torsion in the inverted position thus offers a further confirmation of the statolith-theory.

CHAPTER XXXVI

EFFECT OF UNILATERAL STIMULATION ON AUTONOMOUS TORSION

THE experiments already described show how diverse are the influences which modify the autonomous torsional movement of plants. I describe some of the important factors in operation during the course of the day and their individual effects.

Effect of variation of turgor.—An increase of turgor induces an enhancement of the normal rate of torsion, while a diminution causes a retardation culminating in a reversal. Turgor may be increased (*a*) by enhanced rate of ascent of sap, or (*b*) by increased moisture in the air (dependent on the direction of the wind); diminished turgor is, on the other hand, produced by drought due to transpiration increased by dry air, by high temperature, and by strong sunlight.

Effect of variation of temperature.—Rise of temperature up to an optimum enhances the rate, while increasing cold induces a retardation. A rapid variation of temperature acts as a stimulus and induces a reversal of direction.

Effect of stimulation.—The following is true of all modes of stimulation. Feeble stimulation causes an enhancement in the normal rate, while strong stimulation causes a retardation culminating in a reversal. The effect of stimulation is modified by its point of application, direct stimulation producing one effect, indirect stimulation giving rise to an effect precisely the opposite.

Effect of light.—The intensity of light during the day undergoes continuous variation. It increases from dawn to noon and declines from noon to evening. The effect of

increasing intensity of light is retardation of the rate of torsional movement, which may culminate in reversal. The retarding effect ceases under diminished intensity of light.

Effect of gravitational stimulus.—Gravity also has a pronounced effect on torsional movement, which is dependent on the angle of inclination.

A continuous fluctuation of torsion occurs as the resultant of these different factors; some of them are concordant in their effect, thus increasing the normal movement, while others diminish or even reverse it. The record of torsional movement taken for a long period thus appears to be highly erratic, a sudden increase being followed by an equally abrupt reversal.

Diurnal Variation of Torsion

I give an automatic record (fig. 223) taken continuously for 24 hours, the movement being reduced to keep the tracings within the limits of the smoked glass plate. The experiment was carried out under relatively simple conditions. A young internode of a stem of Thunbergia was clamped at the node below, and held erect in the manner already described (p. 385). The shoot was introduced, through a hole in a table, into a glass chamber which protected the recording apparatus from disturbance caused by air-currents. Ground glass was employed for the cover, to give a more uniform illumination during the day. The record was commenced at 4 P.M. and continued for 24 hours. Light was at that time disappearing, the retarding effect of light being thus removed; the temperature, very high at thermal noon, had fallen to the optimum at about 4 P.M. Owing to these two concordant factors, the direction of torsion was positive, that is, anti-clockwise. After 9 P.M. the fall of temperature was rapid and the torsional movement underwent a slight reversal up to early morning. From 6 A.M. onward, the temperature rose above 20° C. and light increased. The effect of rise of temperature was predominant, so that the

rate of positive torsion increased rapidly. At noon the temperature rose to 42°, very much above the optimum, and the retarding effect of the strong light was very great. The

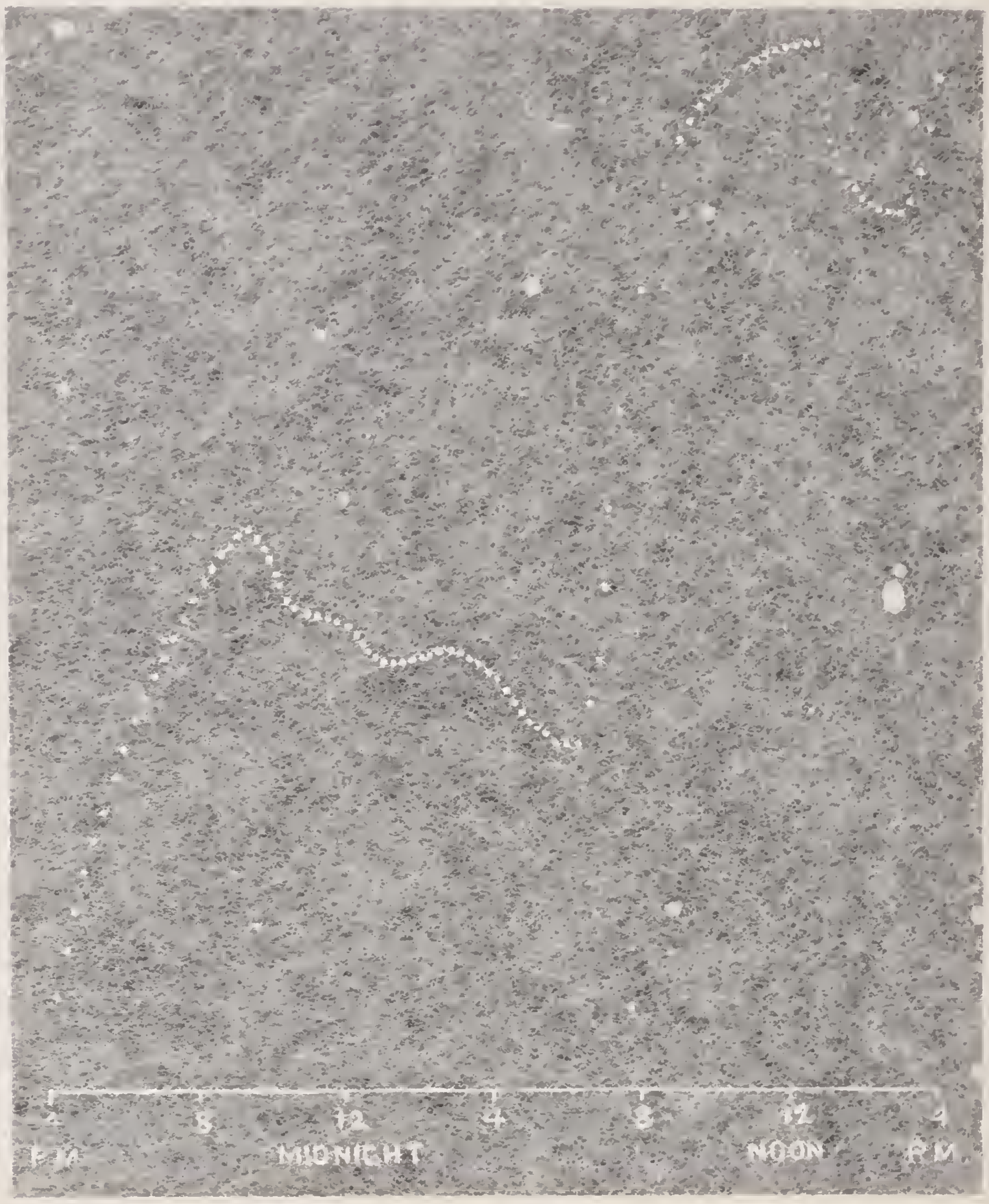


FIG. 223. Automatic record of diurnal variation of torsion.

condition of drought caused by excessive transpiration also conspired to induce a reversal of direction from positive anti-clockwise to negative clockwise movement. This continued till 3 P.M., after which time the record shows a repetition of what occurred 24 hours before.

EFFECT OF UNILATERAL STIMULATION BY LIGHT

In the previous chapter I described the effect of stimulation by light applied simultaneously on all sides of an anisotropic

twisting organ. The modification of torsion produced was due to the differential excitability of the two longitudinal halves of the organ. In the case of the stimulus of gravity stimulation is also diffuse in the erect and in the inverted positions. But a new class of phenomena makes its appearance when the two flanks of the anisotropic organ are successively excited by lateral stimulation. The plane of junction of the two halves of the twisting stem, it is to be remembered, is always undergoing slow revolution (*see* p. 376). The results are of high significance, though at first sight they appear to be contradictory. I will first describe the effects of unilateral application of light to the different sides of the organ.

Method of Procedure

The normal rate of torsion is first taken in the dark; the effect is then observed of subjecting the different sides of the organ to a narrow line of light produced by a cylindrical lens interposed in the path of a parallel beam of light from an arc-lamp. The different sides of the organ are successively exposed to light by rotating the small glass bottle in which the specimen is mounted; the angle through which the plant is rotated can be read on the horizontal scale (*cf.* fig. 215).

Experiment 226.—I give detailed results obtained with Clitoria which may be taken as typical. The rate of torsion, when one of the sides was exposed to light, was ascertained; readings of the rate of torsion were next taken when light acted on another side. In the first position the natural rate of torsion in the dark was 30 mm. per 5 minutes. Exposure to light increased it to 35. When the plant was rotated through 22·5°, the rate increased to 45. This increase continued till a maximum rate of 61 was attained. Further rotation of the plant in the same direction now induced an increasing retardation which culminated in

actual reversal to − 4. Further rotation beyond this point restored the direction of torsion to positive and the rate to nearly the same value as when the plant was in the previous position. The results are made clear by the following tabular statement of the rates of torsion in four different positions 90° apart—at 67°, 157°, 247°, and 337°.

TABLE LIV.—EFFECTS OF EXPOSURE OF DIFFERENT SIDES (90° APART) TO LIGHT (PORANA).

[Normal rate in dark = 30.]

Different sides . .	67° (A)	157° (N)	247° (R)	337° (N′)
Rate of rotation	61	29	− 4	27

A careful examination of the above results leads to the following conclusions :

1. The action of light on the different sides of the stem induced responsive torsional variations which are very characteristic.

2. Four different sides can be distinguished by their respective induced variations. Two of these, N and N′, at 157° and 337° in Table LIV, are neutral, the rate of torsion having remained practically the same as when in the dark.

3. The two flanks, at right angles to the neutral sides, exhibited marked changes : the one (A), at 67°, showed a maximum acceleration of 61 ; the other (R), at 247°, showed a maximum retardation culminating in actual reversal to − 4.

I obtained numerous other results in confirmation of the above : the following table gives a synopsis of the effects induced in four other specimens of Clitoria. It is to be remembered that N, N′, and A, R, are at right angles to each other.

TABLE LV.—EFFECTS OF EXPOSURE OF THE DIFFERENT SIDES TO LIGHT

Specimen	Maximum acceleration. A	First neutral. N	Reversal. R	Second neutral. N′
1	12	5	− 4	3
2	32	20	− 2	18
3	11	8	− 4	6
4	21·6	9·5	− 6·5	7·5

The above results, which fully confirm the previous conclusions, were totally unexpected, and appear at first sight to be quite inexplicable.

TORSIONAL RESPONSE OF ANISOTROPIC ORGANS

The difficulty is completely overcome on reference to the Laws of Torsional Response of Anisotropic Organs which have already been established (p. 256), that—

1. *An anisotropic organ, when laterally excited by any stimulus, undergoes a torsion by which the less excitable side is made to face the stimulus.*

   My present results extend this generalisation to differentially growing organs also, and the wider inclusive law is enunciated as follows:

2. *A differentially growing organ, when laterally stimulated, undergoes a torsion by which the less excitable side is made to face the stimulus. The induced torsional movement is algebraically summated with that of the existing autonomous torsion.*

The parallel results in differentially excitable pulvinated and in differentially growing organs will be clearly understood from the following illustrative examples.

TORSIONAL RESPONSE OF THE PULVINATED ORGAN

The diagram (fig. 224) will explain the principal effects. The shaded lower half of the pulvinus is the more excitable, and the plane of junction of the two halves is marked

on the flanks by A and R. The neutral sides are N, N′. If a stimulus, light for example, acts from above on N, an up-movement due to positive phototropism will occur; if from below, a more pronounced down-movement due to the greater excitability of the lower half. No torsional movement will, however, occur on stimulation of N or N′. But the results will be different when stimulation is applied

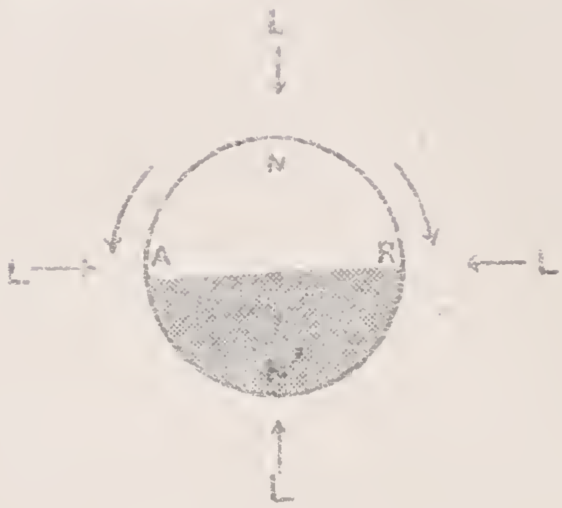


FIG. 224.

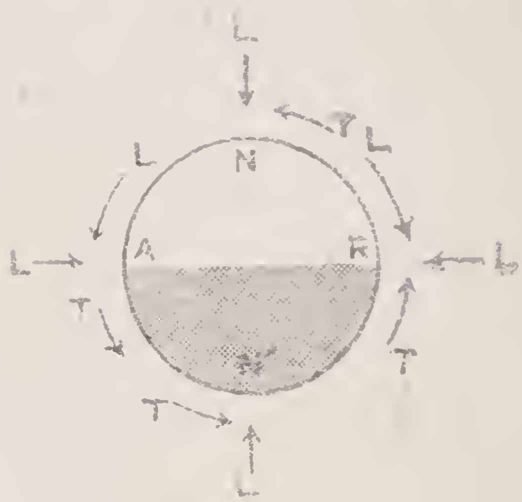


FIG. 225.

Diagrammatic representation of torsional response of anisotropic organs to unilateral stimulation by light L.

Ideal transverse sections of the organs: N, N′, ventral and dorsal sides; A, R, flanks: A–R, plane of junction of the two diverse longitudinal halves, of which the more excitable is shaded.

FIG. 224. Pulvinus of Mimosa: Stimulation of sides N, N′, evokes no torsional response; stimulation of flank A induces positive (anti-clockwise) torsion (left curved arrow); stimulation of flank R induces negative (clockwise) torsion (right curved arrow).

FIG. 225. Twisting Stem (supposed erect). Normal torsion, T, unaffected by stimulation of sides N, N′; increased on stimulation of flank A, decreased on stimulation of flank R.

laterally to either flank A or R. Lateral stimulation of flank A induces a torsional response against the hands of the clock, the less excitable upper half being moved so as to face the stimulus. This will be distinguished by a *positive* sign. Lateral stimulation of the opposite flank R induces a *negative* or clockwise torsion.

TORSIONAL RESPONSE OF THE TWISTING STEM

The effects of unilateral stimulation by light on the autonomous torsion of the twisting stem are much the

same as those observed with the anisotropic pulvinus, but with the difference that the torsion induced by the unilateral action of light on the different sides of the stem is algebraically summated with its autonomous torsion. This is made clear on inspection of fig. 225, in which the shading indicates the more excitable half. The straight arrows indicate the direction of the light incident on the four sides, N, A, N′, and R. The arrow T indicates the natural torsion. Light incident on the neutral sides N or N′ induces no torsional effect, but there may be a slight rectilinear movement up or down due to positive phototropism. The torsion induced by light falling upon either flank, A or R, is maximum, and is algebraically summated with the natural torsion. That induced by light falling on flank A co-operates with the natural torsion: that induced by light falling on flank R opposes the natural torsion and may even overpower it, so that it is not only retarded but the direction is reversed.

The results obtained show that there is no ground for the assumption that twining plants possess a specific sensibility to light different from that of ordinary plants. The variation of torsional movement due to the action of unilateral light on different sides of the organ results from the differential excitability of the organ, the characteristics of which conform to the Law of Torsional Response in all anisotropic organs.

A few words may be added in regard to the conditions for securing the best result. These are: (1) quick determination of the maximum position A, and (2) completion of the whole series of observations for N, R, and N′ within a short time. For the plane of junction is not stationary but slowly revolving, and can only be regarded as stationary for a relatively short time. It is also desirable to take only a short length of the stem for the observation of torsional movement, so that the plane of junction of the two halves of the organ is vertical and straight.

I shall next show that the effect of unilateral stimulation by gravity is essentially similar to that induced by light.

Effect of Unilateral Stimulation by Gravity.

As the direction of stimulus of gravity is fixed, the different sides of the twisting stem can only be exposed to it by

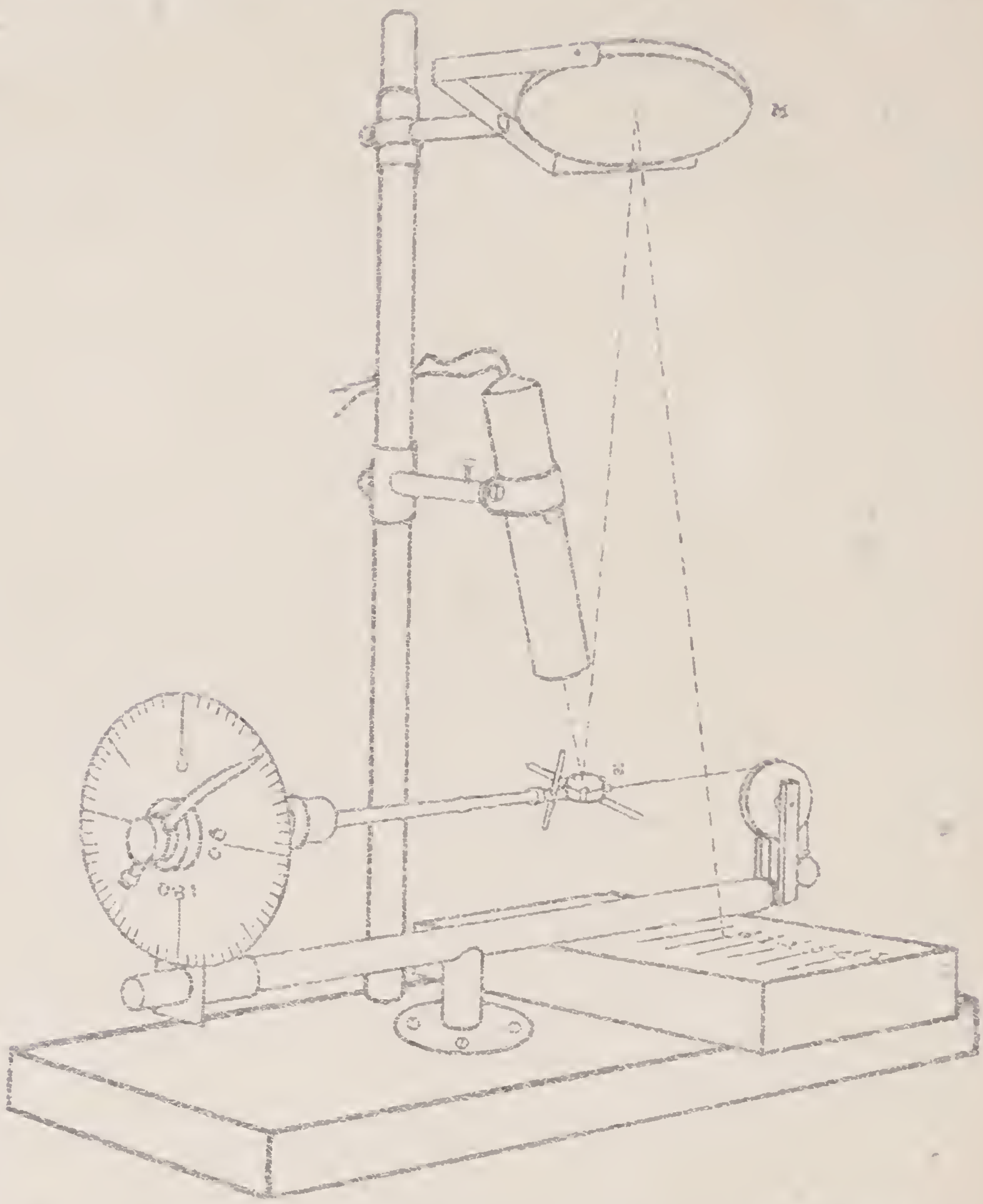


Fig. 226. Optical Method of observing rate of torsional movement under unilateral stimulation by gravity. The different sides of the horizontally laid stem are exposed to vertical lines of force of gravity by rotating the plant-holder with attached index, the angle being measured by the circular scale.

rotating the horizontally laid stem round its axis. The diagrammatic representation of the apparatus explains the method of observing the rate of torsional movement. The different sides of the organ are subjected to the stimulus of gravity G, by rotating the small cylindrical vessel of

water in which the lower end of the stem is fixed. This water-vessel is shown to pass through the fixed circular scale, the angle of rotation being measured by means of the index attached to the vessel (fig. 226).

The torsional response to unilateral stimulation by gravity is, as in the case of light, not the same for all the sides, but shows characteristic differences, as will be seen from the results of the following experiment.

Experiment 227.—The stem of Clitoria was rotated till the maximum rate of positive torsion was obtained, indicating the A position. Representing the natural rate by T,

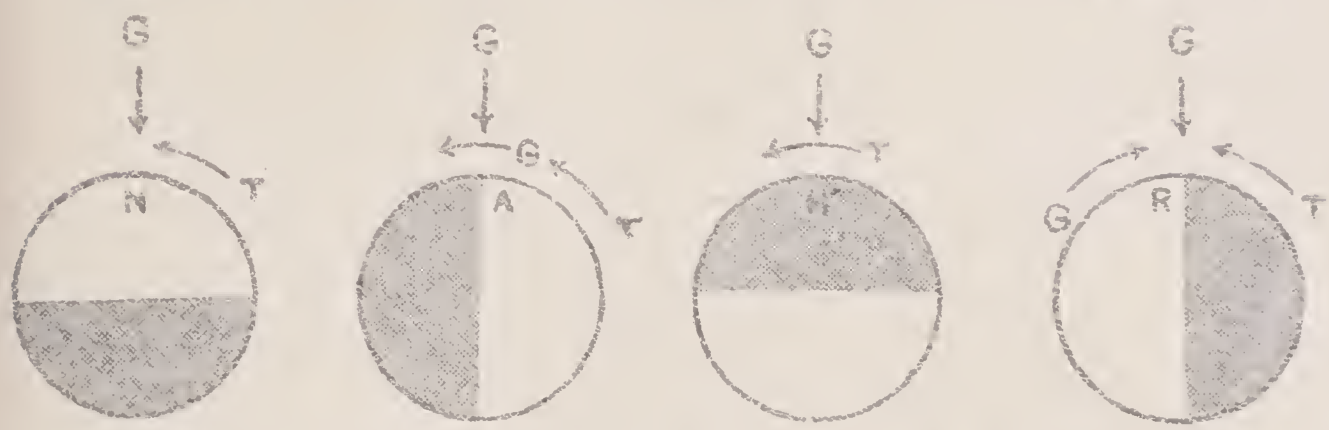


FIG. 227. Torsional response of the stem to stimulation of its different sides by gravity in four positions, N, A, N', R. No effect at N, N'; effect at A, additive; at R, in opposition. T, normal autonomous torsion; G, gravity.

and by G the torsion induced by geotropic stimulation, the result is the summated effects T + G, which in the present case was 42. The plant was next rotated through 90°, bringing it to N position, in which the torsional response induced by G declines to zero. The response was now 7. Further rotation through 90° brought the plant to the R position; now the induced torsion was *negative*, and it overpowered and reversed the natural torsion, the resultant T − G being − 24. Further rotation through 90° brought the stem to the second neutral position N′, the rate being 5, which is not very different from 7, which was the rate at the first neutral position N.

A large number of other experiments carried out with different species of plants gave very similar results, of which

a diagrammatic representation is given (fig. 227). The following tabular statement gives a synopsis of results with four specimens, two of Porana and the other two of Thunbergia.

TABLE LVI.—EFFECT OF UNILATERAL GEOTROPIC STIMULATION.
(T = auto-torsion; G = induced torsion under gravity.)

Specimen	A T + G	N or N T	R T − G
1. Porana	74	9	− 60
2. Porana	80	33	− 15
3. Thunbergia	135	55	− 28
4. Thunbergia	25	7	− 12

The results of the experiments on the effect of unilateral stimulation by gravity show that there is nothing to support the assumption of three types of geotropic reaction in twining stems, negative, dia-geotropic, and lateral. The results, on the other hand, demonstrate the characteristic effects of diffuse and of unilateral stimulation on anisotropic organs. In the vertical and erect position, the natural rate of torsion is slightly retarded by the diffuse action of geotropic stimulation, the statolithic particles pressing on the basal end of each statocyst. In the vertical but inverted position, the effective stimulation is intensified on account, presumably, of the greater excitability of the apical ends of the cells. The result is an increased retardation which sometimes culminates in an actual reversal of torsion from positive to negative.

The share of geotropic reaction in the movement of a young stem about to twine, of which the lower portion is erect whilst the upper portion overhangs, requires careful analysis. The erect portion twists round its own axis, a movement not affected by gravity, which causes the circumnutation of the overhanging portion. Of this the terminal internode twists but slightly: it tends to curve upwards in response to gravity. In the succeeding internodes torsion is most active, and it is affected by gravity

in a characteristic manner depending upon the rate of revolution of the plane of junction of the two diverse longitudinal halves of the anisotropic stem which necessarily accompanies torsion. If the rate of revolution be such that the flank A is always uppermost, then the autonomous torsion will be accelerated by gravitational reaction. The movement of the stem as a whole will then be composed of (1) the circumnutation, say, anti-clockwise, due to the torsion of the erect portion of the stem, and (2) the circumnutation of the overhanging portion round a more or less inclined axis. This compound movement is not unlike planetary motion in which, in addition to the revolution round its own axis, the planet describes an elliptical path round the sun.

But if the revolution of the plane of junction does not keep pace with the torsional movement of the stem, a lag will occur, the result of which will be an alternate acceleration and retardation of autonomous torsion by gravitational reaction, according as the A or the R flank of the stem faces upwards. An oscillatory torsional movement, positive and negative, will then take place.

Combined Effects of Geotropic and Photic Stimulation

Having ascertained the individual effects of stimulation by light and by gravity of the different sides of the organ, it is possible to predict their effects in different combinations, taking examples which exhibit strongly contrasted effects. Since the stimulus of gravity is unchangeable in direction, the stimulus of light is superposed on it either from above or from below. The horizontal stem is adjusted in darkness till the rate of torsion is maximum, that is, in the A position in which autonomous torsion and geotropic reaction are concordant, represented by the symbol T + G. By means of two inclined mirrors, a beam of light from an arc-lamp is then thrown upon it alternately from above and from below. In the first case, the action of light co-operates

with that of T + G, the combined action of T + G + L giving rise to a large positive or anti-clockwise torsion. In the second case, light acts in opposition, the resultant action being T + G − L. Now, if the light be sufficiently intense, it will overpower T + G, and the resultant will be a *negative* or clockwise torsion. The theoretical result is diagrammatically represented in fig. 228, where, in the A position,

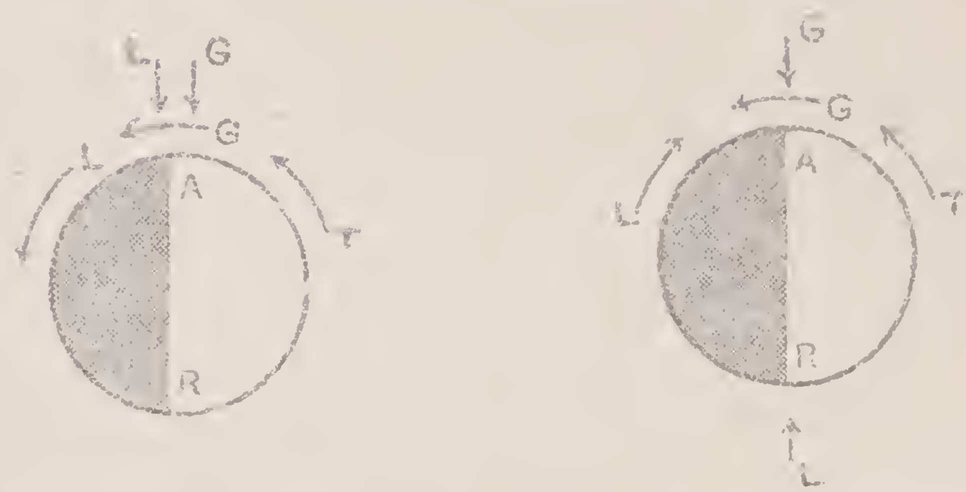


FIG. 228. Combined effects of simultaneous geotropic and photic stimulation on autonomous torsion T.

Light, L, alternately applied above or below (straight arrow). Induced torsion (curved arrow) under light L and gravity G.

the unshaded half to the right is the less excitable. In the figure to the left, light L and gravity G act from above; their additive effect co-operates with autonomous torsion T. In the figure to the right, G acts from above on the flank A, while light acts from below on the opposite flank R. The torsion induced by L is therefore in the opposite direction to that induced by G.

Experiment 228.—Thunbergia placed in A position

1. Rate of torsion without light, T + G = 16
2. ,, ,, with light from above, T + G + L = 40

Light withdrawn; complete recovery under T + G = 16

3. Rate of torsion with light from below, T + G − L = − 8

Experiment 229.—Porana placed in A position.

1. Rate of torsion without light, T + G = 28
2. ,, ,, with light from above, T + G + L = 5[illegible]
3. ,, ,, with light from below, T + G − L = − [illegible]

The results of the above experiments prove that the effect of light is algebraically summated with that of autonomous torsion, and also with that induced by geotropic stimulation.

SUMMARY

It has been shown that the twining of stems is brought about by circumnutation, which is the expression of autonomous torsion.

The stem being also sensitive to the stimulus of contact, twining takes place when the circumnutating stem comes into contact with a support.

The twisting stem is alike sensitive to all modes of stimulation, electric, thermal, photic, and geotropic.

All forms of diffuse stimulation have a retarding effect on growth.

The twisting stem is an anisotropic organ, the two diverse longitudinal halves of which are unequally excitable. Diffuse stimulation induces greater retardation of growth in the more active half, which reduces the normal rate of torsion even to reversal of direction.

Under lateral stimulation by light or gravity, a torsional response is evoked in all anisotropic organs. When the stimulus acts on the A flank, a maximum anti-clockwise movement is induced. The effect of stimulation of the diametrically opposite flank R is a clockwise movement. No responsive torsion occurs on stimulation of the neutral sides N, N′.

The responsive reactions, algebraically summated with the autonomous torsion, explain the varied movements of twisting organs under the simultaneous action of different stimuli.

The reactions to light and gravity are algebraically summated with the autonomous torsion. Light, when sufficiently strong, acting in opposition to gravitational stimulus, induces a reversal of the direction of torsion.

CHAPTER XXXVII

GENERAL REVIEW

THE different chapters of this book describe and discuss observations on the movements of growing organs under the changing conditions of the environment. Some of these, such as variation of temperature and the alternation of light and darkness, affect the rate of growth; others, such as the action of gravity, of unilateral illumination, and of contact with foreign bodies, induce changes in the direction of growth, these changes being generally described as TROPISMS. They are of many kinds and are more or less complex, so that it is no easy matter to analyse them in the hope of arriving at some general principles which would explain them all.

The attempt has been made to account for the movements teleologically, to regard them as determined by the advantage they may contribute to the well-being of the plant, rather than to study them physiologically as manifestations of stimulation and response. It is the latter experimental method which has been pursued in the work here recorded, with results summarised in this chapter.

All movements of growing organs, whether spontaneous or induced, are effected by change in the rate of growth; this change is subject to modification according to the vigorous or feeble tonic condition of the growing organ. It is therefore necessary to have means of immediate measurement of the actual rate of growth and its induced variation.

THE METHOD OF MAGNIFIED RECORD

The *High Magnification Crescograph* permits of the determination of the absolute rate of growth and its induced

variation in the course of less than a minute, during which time other conditions can be maintained absolutely constant. The record shows that growth is a pulsatory phenomenon (p. 18). The Magnetic Crescograph gives an amplification of more than ten million times, thus making possible the measurement of the smallest movement of growth and its slightest variation. The sensitiveness of the method of record has further been increased by the use of the Method of Balance, in which the movement of growth is exactly compensated by an equal movement of the plant downwards, the upsetting of the balance upwards or downwards being due to induced acceleration or retardation of growth. The Method of Balance offers a unique opportunity for determination of the influence of the Time-Factor—that is to say, of the effect on the reaction of the duration of the action of an external agent.

Autonomous Activity of Growth

All autonomous movements are dependent on the following conditions:

1. Sufficiency of internal hydrostatic pressure in the active cells;
2. Supply of energy for the maintenance of the normal tonic condition of the active cells; and
3. An adequate temperature.

Effect of variation in the rate of ascent of sap.—It has been observed in both motile and growing organs that increase or positive variation of turgor, due to enhanced rate of ascent of sap, induces an erection or positive response of a motile organ, and a positive variation or enhancement of the rate of growth. A diminution or negative variation of turgor, due to withdrawal of water, induces a negative response of a motile leaf, and a negative variation or retardation of the rate of growth (p. 55).

Effect of subtonic condition.—When the energy stored for the maintenance of the autonomous activity becomes

depleted, so that the growing organ has become subtonic, growth comes to a standstill. Stimulation is found to revive the activity of the arrested growth (p. 36).

Effect of variation of temperature.—Sudden variation of temperature acts as a stimulus and retards growth; in order to prevent this, experimental thermal change should be gradual. In a number of tropical plants the minimum temperature for arrest of growth is about 22°, the optimum being 34° C. A continuous record of change of growth during uniform rise of temperature gives the THERMO-CRESCENT CURVE from which the absolute rate of growth at any temperature can be obtained (p. 39).

EFFECT OF ANAESTHETICS ON GROWTH

The effect on growing organs of exposure to CO_2, to ether vapour, or to chloroform, is at first expansion and increase in the rate of growth, followed by retardation, even active contraction (pp. 44, 46, 293). Growth in a state of standstill is revived by ether and chloroform, which offers an explanation of the action of anaesthetics in forcing growth of dormant buds in winter. The acceleration of growth by CO_2 in the first stage of its action gives rise to an enhancement of geotropic response, but continued action causes contraction and brings about a reversal of geotropic response, from an up to a down curvature.

RESPONSE TO DIVERSE MODES OF STIMULATION

It has been generally assumed that the effects of diverse modes of stimulation are specifically different. In reality there is no such difference. Perception of stimulus and the consequent reaction arise in all cases from excitation of the sensitive protoplasm. Though in certain cases anatomical structures, such as tactile hairs and pits, and others, facilitate the perception of a particular form of stimulation by causing deformation of the ectoplasm in an effective manner, the normal results of stimulation are essentially the same whatever the stimulus employed. The first effect of

growing organs is retardation of the rate of growth; if the stimulus be intensified or the stimulation prolonged, the contractile reaction of retardation is more marked, and, at a critical point, causes complete arrest.

The independent method of electrical investigation fully confirms the results obtained by the mechanical method. The closest parallelism has been established between the mechanical and electric responses in both non-growing and growing organs under stimulation. Conditions which evoke negative mechanical and electric response in a non-growing organ, also give rise to negative variation and retardation of the rate of growth. Other conditions which cause positive mechanical and electric response in a non-growing organ bring about positive variation or enhancement of the rate of growth. The physiological machinery is the same in pulvinated and in growing organs.

Effects of feeble and strong stimulation.—It may be said in general that two opposite effects are induced in growth under feeble and strong stimulation. There is a critical intensity below which there is an acceleration and above which there is a retardation. This critical intensity varies in different species of plants. These opposite effects are exhibited in all modes of response to diverse methods of stimulation.

Effect of electric stimulation.—In normal conditions, direct stimulation induces incipient contraction exhibited by a retardation of the rate of growth; this is sometimes effected by an intensity of stimulus below the range of human perception. Under increasing intensity of stimulation the contractile reaction becomes more and more pronounced. At a critical intensity of stimulus, growth becomes arrested; under a still stronger intensity there is an actual shortening of the organ. A continuity thus exists between incipient and actual contraction.

Effect of mechanical stimulation.—Moderate frictional stimulation induces incipient contraction, manifested as retardation of growth, recovery being completed within a

short time, but intense stimulation caused by a wound gives rise to a greater and more persistent retardation of growth (p. 89).

Effect of photic stimulation.—The normal effect of light is an incipient contraction or retardation of growth. The after-effect of brief and moderate stimulation by light is an acceleration of growth above the normal rate. The effectiveness of the different rays of the visible spectrum in retarding growth undergoes a decline from the blue to the yellow-red (p. 78).

Radio-thermal stimulation.—The effectiveness of the infra-red rays in retarding growth undergoes sudden augmentation when the rays of heat are reached (p. 79)

Response to wireless stimulation.—The effect is found to be essentially similar to that under the action of visible light. Under strong intensity of stimulation the response is a retardation of growth. Under feeble intensity of electric waves the response is an acceleration of growth, which is also the characteristic effect of feeble light (p. 189).

Effect of high-frequency alternating field of electric force.—The effect of this is analogous to that of wireless electric waves. The response is modified, as in the case of visible light, by the intensity of stimulation and by the tonic condition of the tissue; feeble stimulation induces an acceleration, while strong stimulation causes a retardation, of growth. These facts offer a satisfactory explanation of the anomalous results obtained by different observers on the effect of high-tension alternating current on growth.

Effect of Tonic Condition on Response

The sign of response, negative or positive, is dependent on the tonic condition. Mimosa in a subtonic condition responds to stimulation by an abnormal positive or erectile movement instead of by the normal negative fall of the leaf. Under continuous stimulation the tonicity is raised to a condition of par, the abnormal positive response being now replaced by the normal negative. The effect of stimulation

on growth is modified in a similar manner; the organ in a subtonic condition responds to stimulation by enhancement of its feeble rate of growth: in extreme cases growth at standstill becomes revived under stimulation. Continuous stimulation transforms the response from abnormal acceleration into normal retardation. This is equally true of photic and of electric stimulation (p. 86).

Opposite Effects of Direct and Indirect Stimulation

Stimulation gives rise to dual impulses: the *positive*, which is of a hydraulic nature, not so dependent on the conductivity of the tissue as is the excitatory negative, is transmitted quickly; the *negative*, which is the propagation of protoplasmic excitation, is conducted slowly. The positive impulse gives rise to expansion, positive electric response, and acceleration of the rate of growth. The excitatory negative impulse causes contraction, negative electric response, and retardation of the rate of growth. The negative reaction is more intense than the positive, so that when the intervening distance between the point of application of stimulus and the responding organ is sufficiently small, the positive response is masked by the predominant negative. When the intervening distance is considerable, the negative impulse lags behind the positive, and the response is diphasic, positive followed by negative. When the distance to be traversed is still greater, the excitatory negative impulse becomes weakened to the point of extinction; consequently the hydraulic impulse alone is effective and the response is positive, as shown by the movements of various motile leaves and by an enhanced rate of growth in growing organs (pp. 124, 131).

Tropic Movement under All Modes of Unilateral Stimulation

The difficulty in arriving at an explanation of the diverse effects induced by unilateral stimulation is attributable to

the want of knowledge of the important part played by direct and indirect stimulation, and by the conduction of excitation across the organ. The directly stimulated proximal side of the organ exhibits excitatory contraction, electromotive change of galvanometric negativity, diminution of turgor and retardation of rate of growth; the distal side which is indirectly stimulated exhibits, on the other hand, expansion, electromotive change of galvanometric positivity, increase of turgor, and enhancement of the rate of growth. Positive curvature towards the stimulus is thus caused by the joint effects of the contraction of the proximal and expansion of the distal side. The fact that stimulation of one side of the organ causes an increase of turgor at the diametrically opposite distal side has been demonstrated by stimulation of one side of the stem of Mimosa, which caused the erectile movement of the motile leaf on the opposite side, indicative of an enhancement of turgor (p. 121).

The tropic movement has been vaguely ascribed to change of turgor; but this cannot take place without a definite and active force which determines the direction of flow of sap, causing differential turgor at the two sides of the organ. I have shown that the law which governs the directive movement of sap is that *it follows the stimulation gradient from the stimulated to the unstimulated region.* The turgor is thus diminished at the directly stimulated proximal side from which the sap is expelled, and increased at the distal side where it is accumulated (p. 57).

Transverse conduction of excitation across the organ induces further modification of the normal positive curvature.

Mechanotropism and Twining of Tendrils

Under unilateral mechanical stimulation the directly stimulated side of a tendril undergoes contraction, while the indirectly stimulated distal side exhibits expansion; a positive curvature is thus produced with a movement towards the stimulus, which results in the twining of the

tendril round a support. The after-effect of stimulation of short duration is an acceleration of growth of the stimulated side above the normal, in consequence of which the recovery becomes hastened. Stimulation of one side of the tendril induces expansion of the indirectly stimulated distal side, even in cases where the contractility of the stimulated side is feeble. Hence the response to stimulation of the more excitable side of the tendril may be inhibited by stimulation of the opposite side (p. 99).

PHOTOTROPISM

Quantitative relation.—It has been shown that the amount of phototropic curvature depends (1) on the intensity of light; (2) on the duration of exposure; and (3) on the sine of the directive angle. The intensity of phototropic action is therefore determined by the quantity of the incident light (p. 114).

Dia-phototropism and negative phototropism.—Transverse conduction of excitation to the distal side induces (1) a neutralisation or dia-phototropic response, and subsequently (2) a negative phototropic curvature. An important contributory factor in the reversal of response is the fatigue-relaxation of the proximal side (p. 137).

The effect of light on the root shows that its irritability is in no way different from that of the shoot. In a thick root, in which there is no transmission of excitation to the distal side, the response is positively phototropic, but in a thin root transverse conduction of excitation transforms the positive curvature into negative. Thus, in the root of Sinapis, the sequence of response is positive, dia-phototropic, and finally negative. It was want of knowledge of the preliminary positive curvature that led to the wrong inference that the root possessed an irritability specifically different from that of the shoot (p. 145).

The complete phototropic curve of leaf and of stem consists of four parts: (1) the stage of subminimal stimulation;

(1) the stage of increasing positive curvature reaching a maximum; (3) the stage of neutralisation; and (4) the stage of reversal to negative. The first part of the curve is negative, due to physiological expansion induced by sub minimal stimulation. The curve then crosses the abscissa *upwards*; in the second stage, the *susceptibility* for excitation, feeble at the beginning, increases very rapidly with increasing intensity or duration of stimulation. The positive phototropic curvature then attains its maximum. At the third stage neutralisation occurs. And, finally, at the fourth stage the curve crosses the zero-line *downwards*, the phototropic curvature being reversed to negative.

Phototropic torsion.—Lateral stimulation of any kind induces a torsional response in a dorsiventral organ, the direction of torsion being such that the less excitable half of the organ is made to face the stimulus. Conversely, the direction of an incident stimulus can be determined from the observed direction of torsional movement. The torsional movements of leaves and leaflets of many plants are explicable on the above general principle. The excitatory efficiency of two different stimulations can be compared by the Torsional Balance, by observing the resulting effect when the two stimuli act simultaneously on opposite flanks in the plane of junction of the more and less excitable halves of the anisotropic organ (p. 257).

Photonastic curvature.—There is no line of demarcation between phototropic and photonastic movements; continuity exists between them. By the application of a method of recording the effect of percolation of excitation through the pulvinus of Mimosa, a gradation of excitability has been discovered in the different tissues of the lower half of the organ (p. 163). In an organ with pronounced physiological anisotropy, in which the distal side is far more excitable than the proximal, the transverse conduction of excitation brings about a greater contraction of the distal side. The sequence of response is then positive, neutral and very pronounced negative. Application of stimulus

to the more excitable side of the organ causes predominant contraction of that half, which cannot be neutralised by the transverse conduction of excitation to the feebly excitable other half of the organ. These facts explain the effect of strong light from above causing downward folding of the leaflets of the Averrhoa and upward folding of the leaflets of Mimosa.

Diurnal Movements of Plants

The diurnal movements are the outcome of the co-operation of numerous factors, the most important of which are: (1) thermonastic movement caused by differential growth of two opposite sides of an anisotropic organ under the hourly variation of temperature; (2) the movement due to change in the transpiration-current; (3) the thermo-geotropic response, under variation of temperature, of organs rendered anisotropic by gravitational stimulation; (4) the response of organs sensitive to light under recurrent alternation of light and darkness; and (5) the movements of plants like Mimosa which are sensitive to variation of both light and temperature, and which are also affected by both the direct and the after-effects of light.

Thermonasty.—Thermonastic movements are of two types. The positive is a movement of opening during rise of temperature, the inner side of the organ growing the faster on account of its being the more sensitive. Examples of this are found in Crocus, Zephyranthes, and in European and a few Indian Nymphaeas. In the negative type, rise of temperature induces a movement of closure by the acceleration of the growth of the more sensitive outer side of the organ. The flower of a blue Nymphaea growing in India belongs to this type.

Thermo-geotropism.—This phenomenon was discovered in the investigation of the remarkable periodic up and down movement exhibited by the 'Praying' Palm of Faridpore (p. 224). It was afterwards found to be of wide occurrence, being exhibited by rigid trees as well as by young

stems and by adult leaves of plants. In all these cases an erectile movement is exhibited from thermal noon to thermal dawn, and a movement of fall from thermal dawn to thermal noon. The predominant effect of variation of temperature on the movement is demonstrated by the fact of the abolition of the movement under constant temperature (p. 240). The effect of the stimulus of gravity in inducing the anisotropy which determines the characteristic movement, is proved by the effect on the diurnal record of inversion of the plant (p. 244). The action of thermo-geotropism as an independent factor is proved by its persistence even after the abolition of transpiration (p. 248). The thermo-geotropic movement is in many ways analogous to the thermonastic movement (p. 249). A wider generalisation of thermonasty is reached by the inclusion under it of the movements of full-grown organs which have been rendered anisotropic by the stimulus of gravity.

Diurnal movement due to alternation of light and darkness. The effect of light on the leaflet of *Cassia alata* is predominant as compared with that of temperature. The leaflets begin to close when light is undergoing rapid diminution after 5 P.M., the closure being completed by 9 P.M. This is also partially due to the after-effect of light. The leaflet remains closed till 5 A.M. next morning, after which it begins to open with the dawning light and becomes fully expanded by 9 A.M. The large terminal leaflet of Desmodium exhibits diurnal movements similar to those of Cassia (p. 214).

Diurnal movement of leaf of Mimosa.—The complexity of the diurnal movement of the leaf arises from the fact that it represents the algebraical sum of the effects of three fluctuating factors: (1) the thermo-geotropic action, (2) the immediate effect of light; and (3) its after-effect. With the exception of a small part of the curve in the evening, the diurnal curve of the plant is essentially similar to the typical thermo-geotropic curve, the leaf exhibiting an erectile movement from thermal noon to thermal dawn, and a fall from thermal dawn to thermal noon (p. 269).

The spasmodic fall of the leaf towards evening is not due, as has been suggested, to the increased mechanical moment caused by the forward position of the sub-petioles, for after removal of the sub-petioles the same abrupt fall of the petiole occurs in the evening (p. 272). The evening fall of the leaf is shown to be a post-maximum after-effect of light, which causes an 'overshooting,' so that the leaf falls to below the position of equilibrium (p. 278).

GEOTROPISM

The obscurity surrounding the reaction to geotropic stimulation arises from lack of definite knowledge in regard to the exact direction of the incident stimulus, and as to the character of the response, whether it is contraction or expansion. The direction of the incident stimulus has been definitely determined in two different ways: (1) by observing the effect of superposition of the stimulus of visible light on the geotropically stimulated shoot; and (2) by observing the effect of geotropic stimulation in inducing torsion in the pulvinus of Mimosa, *the less excitable side of the organ moving so as to face the stimulus.* The results of both lines of inquiry are fully concordant, proving that the direction of incident geotropic stimulus coincides with the vertical lines of force of gravity. According to the first method, the geotropic up-movement is enhanced by light acting from above, geotropic and phototropic effects being concordant. Light acting from below induces diminution, neutralisation, or reversal of the geotropic movement, the two forces being now in opposition (p. 288). A similar conclusion is arrived at by the method of geotropic torsion (p. 308). This evidence, that in a horizontal shoot the upper side becomes stimulated by gravity, is confirmed by the excitatory reaction of that side which is an induced electromotive variation of galvanometric negativity (p. 315). The electric response of the lower side is one of galvanometric positivity indicative of enhancement of turgor and

increased rate of growth. The method of geo-electric response is more sensitive in the detection and quantitative determination of the effect of stimulation by gravity than that of mechanical response.

Localisation of geo-perceptive layer.—The induced galvanometric negativity of the upper side of the shoot when stimulated by gravity is not uniform in the different tissues of the organ. The excitatory reaction attains a maximum value at a definite layer, beyond which there is a decline. This is the geo-perceptive layer which has been localised by measuring the depth of intrusion of the exploring Electric Probe at which maximum deflection of galvanometric negativity is detected. The geo-perceptive layer thus localised is found to be at or near the starch-sheath which contains a number of large-sized starch-grains (p. 341). In the stem of certain plants the distribution of excitability exhibits two maxima, the focus of excitation being not single but double. Microscopic examination showed that the starch-sheath in these is double and that the positions of the two electric maxima coincide with those of the two starch-sheaths (p. 345). These results afford strong support to the statolith-theory that it is the weight of heavy particles which induces geotropic excitation in the higher plants.

Critical angle for immediate geotropic excitation.—The critical angle has been found in a large number of plants to be about 31·8°. This is additional evidence in favour of the statolith-theory, for the abrupt reaction beyond the critical angle can be most satisfactorily attributed to the sudden fall of particles from the base to the side of the sensitive cells (p. 360).

Geotropism of root.—On subjecting the tip of the root to the stimulus of gravity, the upper side exhibits excitatory reaction of galvanometric negativity (p. 368). This shows that the root-tip, which contains starch-grains, becomes directly stimulated. The electric response in the growing region, above the stimulated point at the root-tip, is positive, indicative of increase of turgor and expansion, showing that

this region has been indirectly stimulated by a transmitted impulse (p. 369). The stimulus of gravity is perceived at the root-tip and the responsive movement takes place at the distant growing region. In contrast with this is the fact that the growing region of the shoot is both sensitive and responsive to geotropic stimulation. As the effects of direct and indirect stimulation on growth are antithetic, the responses of shoot and root cannot but be of opposite sign. There is thus no necessity for postulating two different excitabilities for the shoot and the root; the difference of response is not due to any inherent quality, but to the mode of stimulation, direct in the one case, indirect in the other.

Difference between effects of geotropic and photic stimulation of the root.—In phototropism, the energy of light directly stimulates the responding cells of the growing region, causing a curvature towards the stimulus. In geotropism, the force of gravity is in itself inoperative; it is only through the weight of the cell-contents of the perceptive tissue that stimulation is effected at the root-tip. The impulse there initiated travels to and indirectly stimulates the growing region which responds by a curvature away from the incident stimulus.

AUTONOMOUS TORSION

It has been shown that the twisting growing stem is anisotropic, two longitudinal halves at any given moment being unequally active, like the two halves of the pulvinus of Mimosa (p. 376). The plane of demarcation separating the two physiologically diverse halves in Mimosa is fixed; but in the stem the plane slowly revolves, passing from ... segment (p. 393). The resulting torsional growth ... the movement of circumnutation (p. 381).

... in the rate of ascent of sap.—Enhancement ... of ascent induces an increase in the rate ... depression of ascent or plasmolytic withdrawal induces retardation of the rate culminating ... of the direction of torsion (p. 386).

Effect of variation of temperature.—Rise of temperature up to an optimum induces an enhancement of the rate of torsion; lowering of temperature, on the other hand, brings about a depression or an arrest of movement (p. 388). At the critical temperature of about 60° C. there is a sudden reversal of torsional movement indicative of the spasm of death (p. 390).

Effect of chemical agents.—The effect of a moderate dose of ether is a very marked enhancement of the rate of torsion. Chloroform causes a preliminary enhancement of the rate of torsion, followed by reversal and arrest of the movement (p. 393). The preliminary effect of poisonous solutions is an enhancement of the rate of torsion, followed by reversal and final abolition of movement (p. 392).

Effect of Diffuse Stimulation on Autonomous Torsion

Feeble stimulation, whether electric, mechanical or photic, enhances the rate of torsion, whereas strong stimulation retards it even to actual reversal (p. 396).

The effect of indirect stimulation is an enhancement of the rate of torsion (p. 399).

In regard to photic stimulation, the effect of red light is an enhancement of the rate of torsion, while blue light causes a marked retardation (p. 402).

Geotropic stimulation.—When the organ is held upside down, the rate of normal torsion undergoes retardation, which may even culminate in the actual reversal of the torsional movement, proving that geotropic stimulation is more effective in the inverted position. F[illegible] already been adduced which appear to sho[illegible] excitability of the ectoplasmic layer is greater [illegible] end of the geo-perceptive cell than at the base[illegible] In an inverted position the heavy particl[illegible] with good reason supposed to cause geotro[illegible] press against the apical ends. The retarda[illegible]

in an inverted position thus offers an important confirmation of the statolith-theory.

Effect of Unilateral Stimulation on Autonomous Torsion

Action of light.—The effects of light on different sides of the twisting organ are unequal. There are two sides, N, N′, which are neutral, exhibiting no responsive variation of torsion under stimulation. The two flanks A and R, at right angles to N, N′, are, however, highly sensitive, stimulation of A inducing maximum acceleration, while stimulation of R causes maximum retardation (p. 410). All the varied results are included under the Law of Torsional Response that has been established: *A differentially growing organ laterally stimulated undergoes a torsion by which the less excitable side is made to face the stimulus. The induced torsional movement is algebraically summated with that of the existing autonomous torsion.*

Action of stimulus of gravity.—The effects under geotropic stimulation are precisely similar to those of photic stimulation—that is to say, there are two sides, N, N′, which are neutral, whereas the effect of stimulation of flank A causes a maximum enhancement of the rate of torsion, and stimulation of flank R induces a maximum retardation culminating in reversal.

Combined effects of geotropic and photic stimulation.—The experimental results prove that the effect of geotropic stimulation is algebraically summated with that of photic stimulation, thus inducing a variation in the rate of torsion (p. 415). Light, when sufficiently strong, acting in opposition to gravitational stimulus, may thus induce a reversal of the direction of torsion.

In conclusion it may be stated summarily that the experimental evidence adduced in the foregoing chapters, as to the nature and conditions of the growth-movements, makes it possible to explain their mechanism in a simple and comprehensive manner. The growth-movements are

often complex, owing either to the organisation of the organ, as, for instance, when it is anisotropic, or to the fact that they are the resultants of simultaneous action of two or more stimulating agents. But it has been shown that such complex movements are susceptible of analysis, and can then be adequately accounted for on general principles.

The fundamental principle is that growth is retarded by strong and accelerated by weak stimulation of whatever kind. Closely connected with it is the further principle that direct stimulation retards and indirect stimulation accelerates the rate of growth: this is the essential feature of the mechanism of tropisms. There is no longer any ground for assuming distinct irritabilities, such as the phototropic and the geotropic, or negative and positive phototropism and geotropism: these terms may remain as merely descriptive of the visible response. There is but one irritability of the growing organ which responds to all stimuli that may act upon it, and in essentially the same manner.

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